МОРСЬКИЙ ЕКОЛОГІЧНИЙ ЖУРНАЛ

УДК: 582.26:581.1

PHYTOPLANKTON CARBON TO CHLOROPHYLL *a* RATIO: RESPONSE TO LIGHT, TEMPERATURE AND NUTRIENT LIMITATION

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Поступила 5 февраля 2003 г.

A review was carried out on the effects of light, temperature and nutrient limitation on the carbon to chlorophyll *a* ratios of 36 microalgae species from 7 taxonomic groups using the literature and our own experimental data. Under similar conditions the C:Chl *a* ratio for individual taxonomic groups increase in the order: Chlorophyceae < Bacillariophyceae, Prochlorococcus < Prymnesiophyceae < Cyanophyceae < Dinophyceae. At constant temperature, the C:Chl *a* ratio increases linearly as light increases and decreases exponentially as temperature grows at constant light level. The combined effect of irradiance and temperature on C:Chl *a* ratio is described using an equation with 3 coefficients. From the empirical equation a decrease in the light levels causes a decrease in the effect of temperature on the C:Chl *a* ratio. In all algae groups studied different light levels increases the C:Chl *a* ratio in the same way under nutrient limitation. Taking into account, the taxonomy of the phytoplankton, nutrient limitation of phytoplankton growth rate, temperature and light intensity the C:Chl *a* ratio within the mixed layer in the oligo-, meso- and eutrophic waters of the tropical Atlantic Ocean was 145, 96 and 37 gC gChl a^{-1} respectively. Near the base of the euphotic zone the ratio was 30 gC gChl $a^{-1.}$ From the developed equation the C:Chl *a* ratios in phytoplankton under different environment conditions can be described.

Key words: carbon:chlorophyll *a* ratio, light, temperature, nutrient-limitation, photoacclimation, microalgae

Выполнено обобщение литературных и собственных экспериментальных данных по действию света, температуры и биогенных элементов на отношение углерод-хлорофилл *a* в клетках 36 видов водорослей из 7 таксономических групп. При одинаковых условиях средние значения С:Хл. отношения для отдельных таксономических групп увеличиваются в следующем порядке: Chlorophyceae < Bacillariophyceae, Prochlorococcus < Prymnesiophyceae < Cyanophyceae < Dinophyceae. При постоянной температуре С:Хл. отношение повышается линейно с увеличением света и уменьшается экспоненциально с ростом температуры при одинаковой интенсивности света. Комбинированное действие света и температуры на С:Хл. отношение у всех исследованных водорослей описано одним уравнением с 3 коэффициентами. Согласно эмпирической модели, действие температуры на изменение С:Хл. отношения снижается с уменьшением интенсивности света. У всех таксономических групп водорослей при недостатке азота в среде С:Хл отношение увеличивается одинаковым образом при разных интенсивностях света. Создана модель, учитывающая комбинированное действие света, темпера-

туры и биогенных элементов на изменение С:Хл. отношения у микроводорослей. Располагая данными по распределению таксономического состава фитопланктона, концентрации биогенных элементов, ограничивающих скорость роста фитопланктона, температуры и интенсивности света на разных глубинах в олиго-, мезо- и эвтрофных водах тропической части Атлантического океана, по созданной модели рассчитаны С:Хл отношения в фитопланктоне, которые в верхнем перемешиваемом слое составили 145, 96 и 37 гС гХл a^{-1} соответственно, а у основания эвфотической зоны - 30 гС гХл a^{-1}. Предложенная модель позволяет достаточно точно описать изменение отношения С:Хл у фитопланктона при различных условиях окружающей среды.

Ключевые слова: углерод : хлорофилл *a* отношение, свет, температура, биогенное лимитирование, фотоадаптация, микроводоросли

Investigations of spatial temporal variability of phytoplankton biomass are necessary to understand the primary production processes and role of biogeochemical cycles in the ocean. One of the most widely employed methods for estimating phytoplankton biomass is the measurement of chlorophyll *a* concentration. The standard methods of chlorophyll *a* estimation are quick, convenient and accurate [46]. Measurements of chlorophyll concentration continuously from ships and aircraft, including satellites, is now possible using *in vivo* fluorescence or light pigment absorption methods [25, 56]. The derivation of phytoplankton biomass from chlorophyll values has not been successful because the chlorophyll to carbon ratio in cells is not constant. From the literature the values chlorophyll *a*: carbon ratio (θ) range from < 0.005 to 0.15 of the phytoplankton [22, 28, 33, 83]. These values are determined by physiological adaptation of the microalgae to environmental conditions and can be observed *in situ*. Variability of values for θ of phytoplankton has been documented in vertical profiles [8, 57] and along horizontal transects [6] with flow cytometers used to estimate phytoplankton carbon content.

It is known that the relative chlorophyll content increases as irradiance and nutrient limitation decrease [34]. At a constant irradiance, θ is inversely proportional to temperature [33, 81].

The Chl:C ratio is an important variable in models of microalgae growth as it provides a link between phytoplankton growth and chlorophyll *a* – specific photosynthesis rate [2, 38, 50, 54, 78]. Such models describe the relationships between specific growth rate, carbon-specific photosynthesis rate, Chl:C ratio, and the efficiency of photosynthesis. On the whole, the results of modelling individual species are in good agreement with experimental data, which have enabled the relationships between specific phytoplankton growth rate and θ to be described. However, these models cannot predict change of θ without the description of light-dependent gross growth rate. Recently developed dynamic model of phytoplankton acclimation to light, temperature, and nutrients can account for much of the systematic variability of θ in phytoplankton [39, 40]. The model differs from previous steady-state models and can accommodate non-steady- state conditions. It requires specification of four parameters to describe the light-dependent θ and growth rate under nutrient-saturating conditions at constant temperature. These are the maximum value of θ, the maximum carbon-specific photosynthesis rate, the cost of biosynthesis, and the initial slope of the chlorophyll *a*-specific photosynthesis-light

response curve. The first three parameters are rarely reported in the oceanographic literature due to the difficulty to obtain unambiguous measurements *in situ.* The authors [39] acknowledge the difficulties in extrapolating results of laboratory studies to the ocean. They indicate that despite success in describing growth rates and chlorophyll *a* of cultures over a wide range of conditions, the model may not improve estimates of Chl:C ratio of natural populations because of the considerable interspecific variability in maximum growth rates and maximum chlorophyll *a* contents of phytoplankton species.

Maximum values for θ (θ_{max}) of 0.1 to 0.15 gChl gC^{-1} have been observed in chlorophytes and diatoms [54, 77]. However, in contrast to these taxonomic groups the Dinophyceae and Cyanophyceae are characterized by lower values of θ [11, 28, 30, 71]. Observations for 11 algae species and three cyanobacteria species were used to obtain estimates of parameter values for slope and intercept (θ_{max}) of linear regression of θ^{-1} on irradiance [33]. These data confirm that dinoflagellates contain substantially less chlorophyll *a* than diatoms, but could not characterize θ_{max} and the irradiance dependence of θ for the other open ocean phytoplankton taxa, such as the Prymnesiophyceae, Rhaphidophyceae, *Synechococcus* and *Prochlorococcus*. However, a new data extending the list of examined phytoplankton species are available. This allows a wider comparison to be made of the chlorophyll *a* content from various taxonomic groups of microalgae.

The aim of this study was to examine the phenotypic and interspecific variability of θ in a microalgae and cyanobacteria. Based on the literature and own experimental data, this paper provides an assessment of the variability of θ ratio as a function of light, temperature and nutrient limitation for 36 phytoplankton species from 7 taxonomic groups. Using an empirical approach in modelling, we have attempted to describe the Chl:C ratio (impacted by light intensity, temperature and nutrients), without describing the details of the physiological mechanisms driving the output. The effect of each factor, in various combinations, has been estimated separately. The quantitative relationships calculated from the experimental data demonstrated the universal character of the effects of the above factors on θ, for all phytoplankton species. The analysis is based on steady-state data. It is shown that a single function of temperature and light with five coefficients can account for much of systematic variation of θ in nutrient-limited growth rates cultures. The model predictions are shown to be in agreement with experimental observations. The available data indicate that under similar conditions the Chl:C ratio for individual taxonomic groups decreases about 4 times in the order: Chlorophyceae < Bacillariophyceae, Prochlorococcus< Prymnesiophyceae < Cyanophyceae < Dinophyceae.

Data and methods. All available data for marine and freshwater microalgae have been used to obtain the generalisation of the empirical data on the effect of light intensity, temperature and nutrient limitation on the relative chlorophyll content of cells. Most experiments were carried out in batch cultures, which were periodically diluted with medium to keep them in an exponential growth phase. Chemostats and turbidostats were employed in studies of the effects of nutrients. The phytoplankton cultures

were acclimated to new conditions for a number of days in all experiments. Chlorophyll concentrations were measured from optical density of acetone extracts or from fluorescence. Organic carbon was analysed with a CHN analyser [84]. Where carbon was not directly measured, the contribution of chlorophyll *a* to dry weight was estimated by assuming that carbon was 40 % of organic matter. A variety of light sources were employed in the experiments. Irradiance was measured in μmol photons m^{-2} s^{-1} in most experiments, while in others it was expressed in different units.

We have calculated the total daily irradiance and have standardised the units to Photosynthetic Active Radiance (PAR - mol quanta m^{-2} d^{-1}) using the conversions: 1 lu $h^{-1} \approx 0.2$ mol quanta m^{-2} d^{-1}, 1 $Wm^{-2} \approx 0.41$ mol quanta m^{-2} d^{-1} and 1 foot-candle = 10.76 lux [70]. Only experiments where relative chlorophyll content increased as irradiance decreased were analysed. Figures and tables from published papers were examined; in some cases we have taken values directly from figures if tables were not available. The pooled data set included 62 experiments with microalgae species from 7 taxonomic groups.

Description of irradiance and temperature on carbon to chlorophyll a ratio under nutrient replete conditions. The empirical equation [33] was fitted to observation of θ^{-1} to irradiance:

$$\theta^{-1} = \theta^{-1}_{max} + \beta E \qquad (1)$$

where θ^{-1} is g C g Chl a^{-1}, θ^{-1}_{max} is θ^{-1} at E = 0, β is slope in g C g Chl $a^{-1} m^{2}$ mol photon $^{-1}$ day^{-1}, E is in mol photon m^{-2} day^{-1}.

The dependence of θ^{-1} on irradiance and temperature is based upon the empirical equation presented by Geider [33]:

$$\theta^{-1} = (\theta^{-1}_{max} - bT) + \beta E \exp(-kT) \qquad (2)$$

where θ^{-1}_{max} is value at T = 0 ^{0}C and E = 0, β is coefficient in equation (1), b and k are slopes of the regression of θ^{-1}_{max} and β on temperature (T) accordingly.

Results. Irradiance and temperature impact on the chlorophyll to carbon ratio under nutrient replete conditions. The carbon to chlorophyll *a* ratio linearly increase for algae of different taxonomic groups, when the irradiance flux density increases from 0.04 to 170 mol photon m^{-2} day^{-1} (Table 1).

The determination coefficient ($r^2 > 0.8$) is fairly high for the majority of the above experiments. For algae species contained at similar temperatures the variability was θ^{-1}_{max} which was quite low. The average θ^{-1}_{max} was equal to 27.5 ± 1.4 for 6 experiments carried out with *Skeletonema costatum* at 15 to 16° C and for *Phaeodactylum tricornutum* it was equal to 14.8 to 14.9 at 23 to 25° C in experiments conducted at three different laboratories. Differences were observed in the C:Chl ratio for different taxonomic groups. Minimal numbers were observed for Chlorophyceae and maximal numbers were noted for Dinophyceae (Table 1). Two orders of magnitude difference (from 0.15 to 44.0) were reported for the β coefficient for different species, at different temperature conditions. In fact, both coefficients increase with the decline of temperature; θ^{-1}_{max} increases linearly, whereas β increases exponentially.

Table 1. Parameter values for fits of Eq.1 ($\theta^{-1} = \theta_{max}^{-1} + \beta E$) to published data

Таблица 1. Значения параметров уравнения (2), рассчитанных по литературным данным

Species	Irradiance*		T*	N*	θ_{max}^{-1} **	β*	r^2 *	Source
1	2	3	4	5	6	7	8	9
Bacillariophyceae								
Skeletonema costatum	4-46	0.5	0	4	30.2(12.2)	43.58(8.7)	0.94	[93]
S. costatum	2-92	0.5	5	7	42.4(4.8)	12.19(2.8)	0.85	
S. costatum	5-80	0.5	10	5	28.6(4.6)	6.97(2.22)	0.85	
S. costatum	5-94	0.5	16	4	27.5(7.0)	7.03(2.19)	0.88	
S. costatum	19-119	0.5	22	4	30.2(4.7)	3.91(1.96)	0.74	
S. costatum	20-130	0.58	15	4	27.4(0.5)	1.10(0.11)	0.98	[23]
S. costatum	5-450	0.58	15	11	25.0(15.5)	2.03(0.59)	0.56	[51]
S. costatum	12-2000	0.16-1	15	30	29.5(6.3)	1.16(0.11)	0.79	[74]
S. costatum	12-1200	1	15.5	4	27.0(6.5)	0.83(0.07)	0.98	[75]
S. costatum	12-603	0.58	15.5	4	28.8(4.5)	1.01(0.19)	0.94	
S. costatum	28-260	0.5	18	4	23.5(4.1)	2.41(0.24)	0.95	[26]
S. costatum	15-650	0.5	20	4	27.7(6.5)	3.06(0.14)	0.99	[17]
Leptocylindricus danicus	6-72	0.37	5	12	33.5(4.0)	22.64(2.32)	0.90	[90]
	6-79	0.37	10	12	34.6(5.8)	17.64(2.65)	0.81	
	7-132	0.37	15	13	28.8(3.2)	7.84(0.88)	0.89	
	6-127	0.37	20	13	28.0(2.3)	2.85(1.01)	0.47	
Thalassiosira weisflogii	30-600	1	18	5	18.1(1.6)	0.92(0.06)	0.99	[24]
T. weisflogii	2-105	0.5	20	6	18.4(2.0)	2.53(0.26)	0.96	[53]
T. pseudonana	14-512	1	18	12	19.7(2.7)	0.87(0.01)	0.97	[33]
T. pseudonana	5-198	1	17.5	9	28.2(8.1)	5.27(0.50)	0.94	[87]
Fragillaria crotonensis	13-154	1	20	10	17.7(2.1)	1.38(0.21)	0.91	[73]
Chaetoceros curvisetus	28-260	0.5	23	4	19.1(2.0)	1.61(0.20)	0.90	[26]
C. socialis	28-260	0.5	19	4	22.0(1.5)	2.11(0.22)	0.96	
Phaeodactylum tricornutum	3-200	0.5	20	5	20.0(2.6)	2.28(0.36)	0.94	[13]
P. tricornutum	1-560	0.5	25	18	14.9(2.8)	1.38(0.17)	0.94	[86]
P. tricornutum	7-230	1	23	6	14.8(2.5)	1.32(0.11)	0.96	[35]
Euglenophyceae								
Euglena gracilis	9-483	1	25	6	10.9(4.5)	0.85(0.16)	0.91	[16]
Chlorophyceae								
Scenedesmus sp.	15-82	1	20	6	23.0(2.7)	1.24(0.18)	0.92	[73]
S. bicellularis	87-700	0.5	22.8	4	6.3(3.0)	1.24(0.15)	0.97	[63]
Nannochloris atomus	1-200	1	23	6	12.8(1.9)	1.57(0.15)	0.92	[36]
Chlorella pyrenoidosa	11-80	1	26	4	9.0(0.2)	0.90(0.06)	0.95	[65]
C. vulgaris	50-2000	1	36	21	14.0(1.1)	0.15(0.10)	0.98	[84]
Prymnesiophyceae								
Isochrysis galbana	30-600	1	18	5	39.4(3.5)	2.60(0.09)	0.99	[24]
I. galbana	50-1000	0.5	25	5	30.0(12.2)	1.58(0.37)	0.86	[5]
Emiliania huxleyi	24-176	0.58	16	5	36.9(7.0)	7.84(1.13)	0.95	[64]
Rhaphidophyceae								
Olisthodiscus luteus	5-407	0.58	15	7	41.4(10.8)	1.35(0.61)	0.49	[51]
Dinophyceae								
Prorocentrum mariae-lebouriae	7-382	0.5	15	5	57.9(30.3)	6.12(2.32)	0.70	[15]
Alexandrium excavatum	32-407	0.58	15	8	61.3(22.3)	4.90(1.14)	0.75	[51]
Gymnodinium galatheanum	20-481	0.75	15	11	60.7(17.9)	5.86(0.65)	0.90	[67]
G. kowalevskii	8-237	0.5	19	4	58.8(16.6)	2.20(0.20)	0.85	[12]

Table 1. Continued…

1	2	3	4	5	6	7	8	9
Exuviaella cordata	10-175	0.5	25	4	51.2(10.8)	1.41(0.14)	0.91	Finenko (unpubl.)
Peridinium trochoideum	10-175	0.5	23	4	52.2(7.3)	1.45(0.18)	0.90	
Cyanophyceae								
Oscilatoria agardhii	20-140	0.66	15	3	39.6(6.9)	11.5(1.31)	0.99	[71]
O. agardhii	10-140	0.66	20	5	39.5(11.5)	7.63(2.20)	0.86	
O. redekii	15-250	1	15	7	44.6(8.0)	6.05(0.60)	0.98	[30]
Spirulina platensis	50-2000	1	36	19	23.2(1.1)	0.16(0.07)	0.99	[3]
Synechococcus WH8103*	10-450	0.58	24	12	36.9(10.1)	1.35(0.41)	0.56	[60]
Synechococcus WH7803	50-2000	1	22	7	50.1(6.5)	1.61(0.28)	0.94	[48]
Prochlorococcus								
Prochlorococcus MED*	7.5-133	0.5	18	4	16.4(8.5)	3.62(1.99)	0.77	[68]
Prochlorococcus Sarg*	1-133	0.5	18	4	20.6(3.2)	4.20(0.69)	0.95	
Prochlorococcus NATL-1*	7.5-133	0.5	18	3	15.6(1.1)	2.09(0.28)	0.98	
Prochlorococcus MED4*	18-450	0.58	24	8	14.2(8.9)	4.08(0.46)	0.93	[60]

* - Irradiance - μmol m^{-2} s^{-1}; D - the proportion of day which is illuminated (for a 12:12 light:cycle, D = 0.5); T - temperature in °C; n - the number of observations; θ_{max}^{-1} - gC gChl a^{-1}; β- gC gChl a^{-1}mol $m^{-2}day^{-1}$; SD (in parentheses) standard deviation of the estimate; r^2 – determination coefficient.

** θ^{-1} is calculated from Chl/cell and carbon/cell using a conversion for *Synechococcus* - 250 fgC/cell and *Prochlorococcus* – 53 fgC/cell [8]

The coefficient (k) numbers for the same species and for different taxonomic groups change from 0.147 to 0.184 (Table 2).

Table 2. Interspecific and taxonomic groups, variability of coefficients describing θ_{max}^{-1} and β relationship with temperature: 1) $\theta_{max}^{-1} = a - bT$; 2) $\beta = ce^{-kT}$

Таблица 2. Межвидовые и таксономические различия коэффициентов, описывающих связь θ_{max}^{-1} и β с температурой

Species and taxonomic groups	No	a	b	r^2	No	c	k	r^2	T	n
Skeletonema costatum	1	34.5(4.1)	0.60(0.20)	0.28	9	28.5	0.147(0.04)	0.47	0-22	12
Leptocylindricus danicus	2	36.8(2.0)	0.45(0.18)	0.76	10	56.2	0.140(0.02)	0.94	5-20	4
Phaeodactylum tricornutum	3	64.0(4.6)	2.03(1.10)	0.64	11	39.2	0.139(0.05)	0.81	20-25	3
Bacillariophyceae*	4	42.0(3.7)	1.07(0.19)	0.72	12	55.1	0.165(0.03)	0.70	5-25	14
Dinophyceae	5	74.7(2.3)	0.96(0.23)	0.81	13	50.0	0.150(0.02)	0.93	15-25	6
Prymnesiophyceae	6	53.5(3.1)	0.92(0.47)	0.79	14	60.8	0.150(0.09)	0.75	16-25	3
Cyanophyceae	7	57.0(6.2)	0.80(0.36)	0.56	15	142.6	0.184(0.03)	0.90	15-36	6
Chlorophyceae	8	17.6(7.2)	0.18(0.58)	0.03	16	35.0	0.148(0.02)	0.92	20-36	5

* Bacillariophycea without *S. costatum*

The variability of (k) is caused by: 1) intraspecific differences, 2) different temperature range in the experiments on the algae, and 3) small number of experiments. Minimal correlation between β and the temperature were observed for *S. costatum*, a species that seems to be distinct from other diatoms. Numbers of β for *S. costatum* from Narragansett Bay and Trondheimsfjord in the Norwegian Sea were as much as 7 times different, although temperature

was the same (Table 1) [74, 75, 93]. The inclusion of *S. costatum* in our analysis caused low correlation between β and T (r^2 = 0.47). Besides that, θ_{max}^{-1} was not dependent upon the temperature (Table 2). Therefore, it seems that *S. costatum* should be treated apart from the other diatoms.

The degree coefficient (k) exhibits minor differences for the other groups (Dinophyceae, Prymnesiophyceae and Chlorophyceae). The averaged correlation between β and temperature is quite high (r = 0.91). In general, for all eukaryotes:

$$\beta = 59.3 \exp [(- 0.166 \pm 0.015) T] \quad r^2 = 0.83 \quad (3)$$

The values of β for Cyanophyceae and *Prochlorococcus* do not differ too much from those of eukaryotes (Table 1), consequently, they can be combined (Fig. 1).

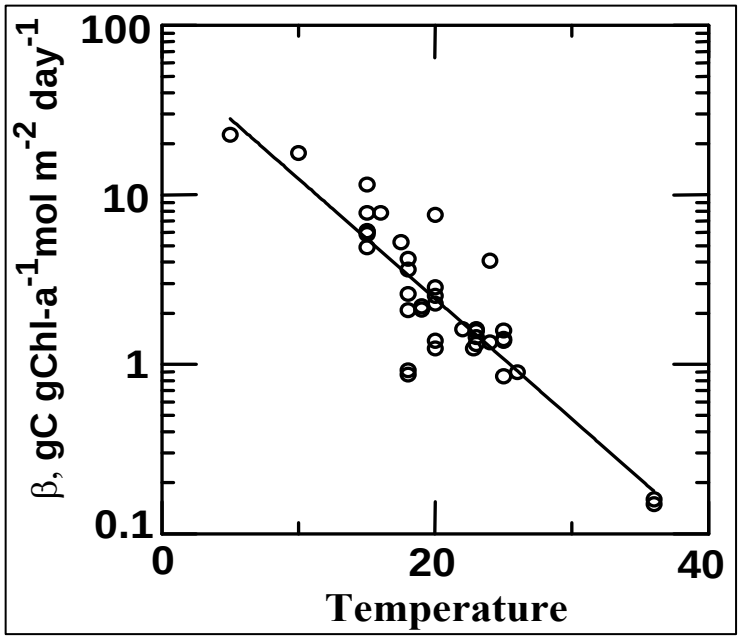

Fig. 1. Relationship between slope of the regression of C:Chl ratio– light (β) and temperature of 36 algae species from 7 taxonomic groups.
Рис. 1. Зависимость между углом наклона регрессии С:Хл отношение – свет (β) и температурой у 36 видов водорослей из 7 таксономических групп.

The unifying equation for 7 taxonomically different groups of algae is as follows:

$$\beta = 63.3 \exp [(- 0.163 \pm 0.01) T] \quad (4)$$

for n = 39; 5 ≤ t ≤ 36° C, r^2 = 0.78.

Numbers of θ_{max}^{-1} increase linearly with the decrease of temperature. The slope of the curve might be different, but it changes in a relatively narrow range, from 0.8 to 1.07 gC gChl a^{-1} for other groups (Bacillariophyceae, Dinophyceae, Prymnesiophyceae and Cyanophyceae, Table 2). The similar type of the relationship and the similarity of coefficients, at relatively high standard deviations, enable the average slope number to be determined, taking into account the population weight:

$$\theta_{max}^{-1} = a - (0.97 \pm 0.02) T \quad (5)$$

where a is given in g C g Chl $^{-1}$ at 0^0 C.

No correlation between θ_{max}^{-1} and temperature in our available data for Chlorophyceae, *Prochlorococcus* and *Skeletonema costatum* were noted. Perhaps this is due to interspecific differences or these algae having different chlo-

rophyll contents within the cell at different temperature and irradiance regimes. If θ_{max}^{-1} does not depend upon the temperature then the carbon to chlorophyll ratio at low irradiance declines by 24 % within temperature range from 15 to 25° C. If θ_{max}^{-1} depends upon the temperature then θ^{-1} would change by 46 %. Differences between both cases would be minimal at irradiance intensities > 10E. The most pronounced differences in averaged θ_{max}^{-1} were observed between algae groups. The number of θ_{max}^{-1} at 25°C, increases about 4 times in the sequence:

Chlorophyceae (13) - *Prochlorococcus* (17) - Bacillariophyceae (17) – Prymnesiophyceae (28) - Cyanophyceae (32) - Dinophyceae (50). Similar numbers are observed for the first three groups (Chlorophyceae, *Prochlorococcus,* Bacillariophyceae,), and groups four and five (Prymnesiophyceae, Cyanophyceae,) could be combined. Substituting into equation (2) the coefficients of equations (4 and 5) and mean θ_{max}^{-1} of algae groups at T = 0° C, an equation describing the combined effect of irradiance and temperature on the carbon to chlorophyll ratio results:

$$\theta^{-1} = (\theta_{max}^{-1} - T) + E\ 63.3 \exp(-0.163\ T) \qquad (6)$$

where θ_{max}^{-1} at temperature 0^0C equally: 41.3 ± 3.9 for *Prochlorococcus* and Bacillariophyceae*;* 54.3 ± 2.9 for Prymnesiophyceae and Cyanophyceae*,* and 74.7 ± 2.3 gC gChl a^{-1} for Dinophyceae*,* T is the temperature and E the irradiance, mol photon m^{-2} day^{-1}.

Estimates of the Chl:C ratio obtained from equation (6) with observed data are compared in Fig. 2.

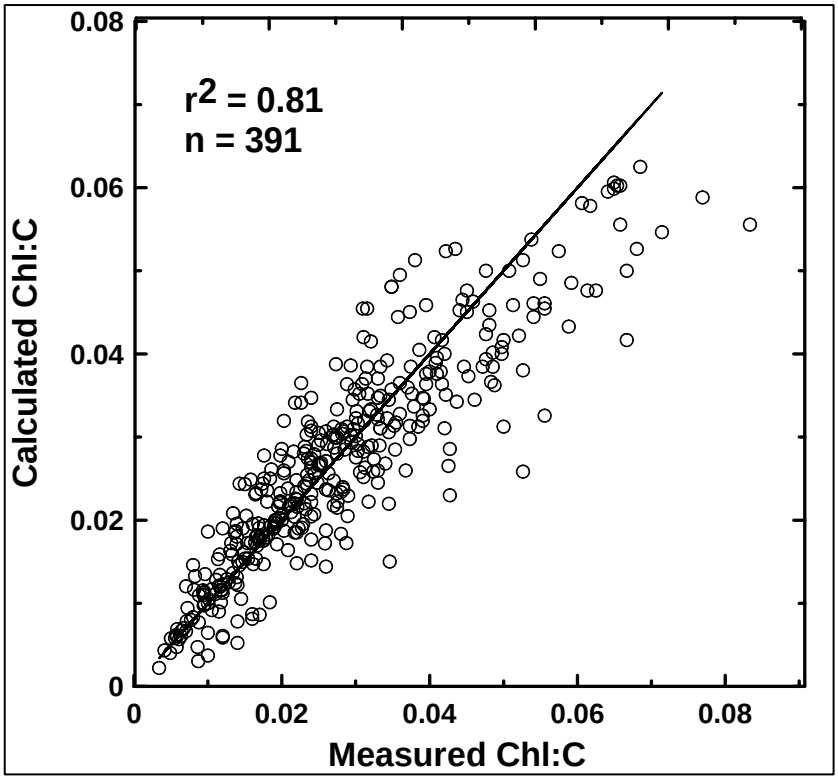

Fig. 2. Comparison calculated Chl:C ratio from equation (6) with observed data. The line shows a 1:1 relation.
Рис. 2. Сравнение рассчитанных Хл:С отношений по уравнению (6)с измеренными данными. Линия показывает отношение 1:1.

The numerical coefficients of equation (1) from Table 2 are used for *Skeletonema costatum*. Data of experiments conducted at 0 to 36°C and at light levels 0.08 to 170 mol photon m^{-2} day^{-1} were extracted from papers cited in Table 1. Coefficient of determination between the computed and measured estimates is 0.82 for all examined species. For the diatoms, 214 measurements were taken, with $r^2 = 0.70$; in other taxonomic groups 177 measurements were taken, with $r^2 = 0.91$. Using the equations given above the derivations are 70 to 90% reliable at recording the light and temperature dependent variability of the Chl:C ratio. Examples are given in Figs. 3 and 4 of predicted light - dependent θ estimates for several species in a series of temperature measurements. Generally, data from experiments conform to the model predictions; measurements differ from the predicted values 2 times to the maximum.

One can see that the function θ (T, E) estimated for Bacillariophyceae, diminishes much faster at low temperatures that at higher ones (Fig. 3). This is associated with the different influence of temperature upon θ^{-1}_{max} and β. The function θ^{-1} (T) exhibits exponential growth, however the carbon-to-chlorophyll ratio diminishes with that of irradiance.

In general, the analysis of the available experimental data has allowed us to show that the carbon to chlorophyll ratio depends not only upon irradiance and temperature but also on taxonomic status.

Nutrient dependence. We have assembled data on algal growth rates (μ) and the chlorophyll to carbon ratio for 9 species from the literature (Table 3).

The growth rates in these experiments have been controlled by the dilution of the algal cultures in the chemostats by the limiting element, i.e. NO_3 or NH_4. It was evaluated that the chlorophyll to carbon ratio decreases when μ declines. Because of different conditions of irradiance conditions in the experiments, we have used the relative growth rates (μ / μ_{max}) and chlorophyll to carbon ratios (θ / θ_{max}), to compare the regression coefficients. Numbers of μ_{max} and θ_{max} are data obtained in each experiment in nutrient replete at this growth irradiance. The correlation coefficient between (θ / θ_{max}) and (μ / μ_{max}) is quite high for all experiments ($r^2 > 0.75$). The slope of the curve changes from 0.7 to 1.09 with an average of 0.9 ± 0.1. The variability of this slope is not associated with the differences of temperature, irradiance and taxonomic composition of the algae used in the experiments. Thus,

$$\theta / \theta_{max} = 0.1 + 0.9\ \mu / \mu_{max}. \qquad (7)$$

for $0.1 \le \mu \le 3$ day^{-1}; $12 \le E \le 1200$ μmol m^{-2} s^{-1} and $r^2 = 0.77$.

The combined effect of irradiance, temperature and nutrients on the chlorophyll to carbon ratio. Under nutrient replete conditions θ inversely related both irradiance and temperature (Eq.6). Nutrient limitation is modelled as having a direct linear relationship with θ / θ_{max} relative μ / μ_{max} (Eq.7). Thus, θ is considered to be a multiplicative function of a nutrient limitation and the dependence of θ on irradiance and temperature as follows:

$$\theta = 1 / [(\theta^{-1}_{max} - T) + E\ 63.3 \exp(-0.163\ T) / (0.1 + 0.9\ \mu / \mu_{max})] \qquad (8)$$

There is good agreement between observed and predicted values (Eq. 8) of θ under nutrient-limited conditions (Fig. 5). The correlation between the calculated and observed numbers is equal to 0.9.

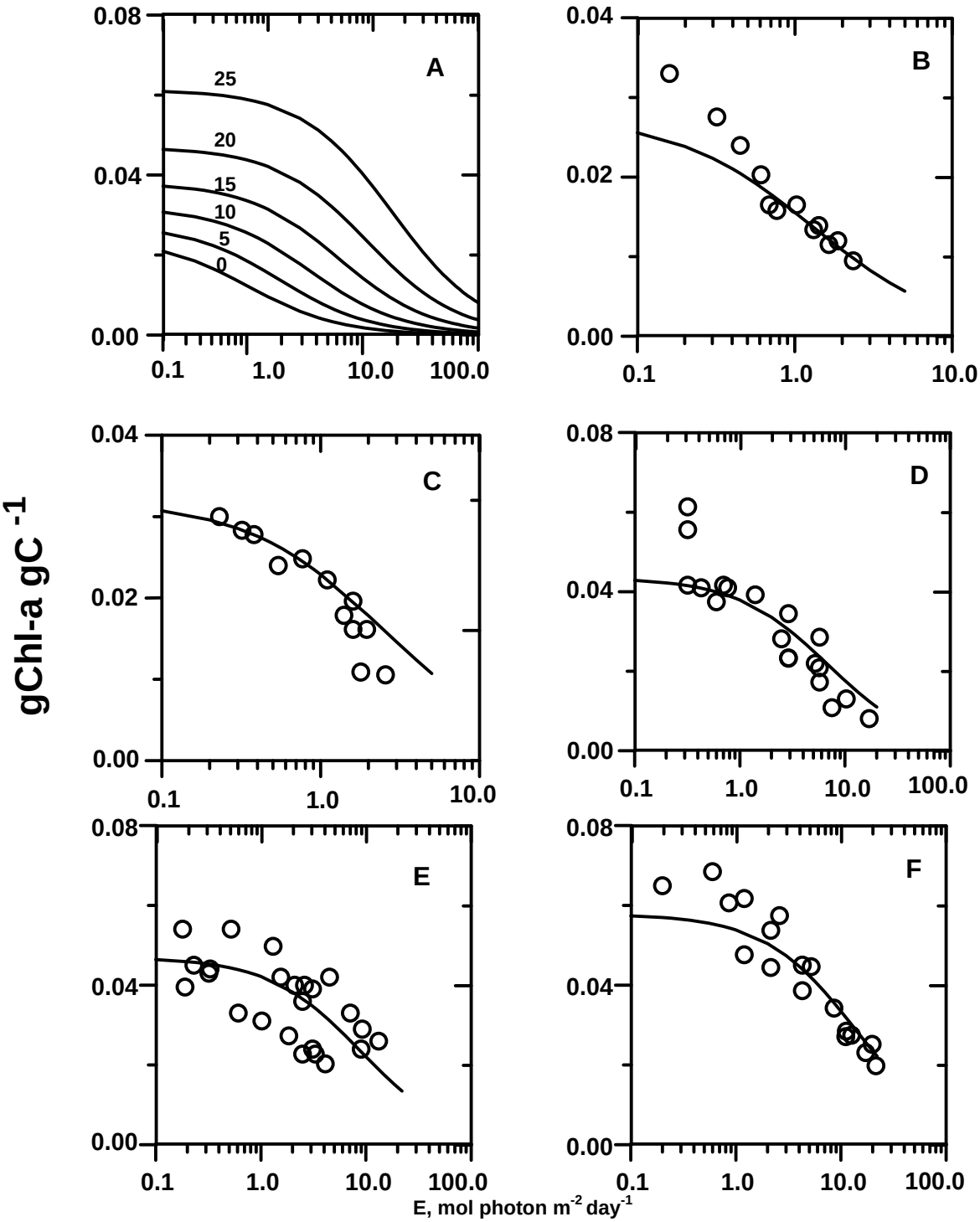

Fig 3. Comparison of model fits (lines) with the chlorophyll to carbon ratio (□) at different growth temperatures and irradiance for the nutrient-replete cultures: Bacillariophyceae and *Prochlorococcus*. (A) - Results of modelling, (B) and (C) - for *Leptocylindricus danicus* grown at 5 (B) and 10^0C (C), (D) - for *Prochlorococcus* MED, Sarg, NATL-1 grown at 18^0C, (E) - for *L. danicus, Thalassiosira weisflogii,Fragillaria crotonensis* grown at 20^0C, (F) - for *Prochlorococcus* MED4, *Phaeodactylum tricornutum* and *Chaetoceros cuvisetus* grown at 23 - 25^0C.

Рис. 3. Сравнение данных модели (линии) со значениями Хл:С отношения (□) при различных температурах и интенсивности света в обеспеченных биогенными элементами культурах: (A) – Результаты моделирования, (B,C) – для культуры *Leptocylindricus danicus*, выращенной при 5 (B) и 10^0C (C), (D) – для культур *Prochlorococcus* MED, Sarg, NATL-1, выращенных при 18^0C, (E) – для культур *L. danicus, Thalassiosira weisflogii, Fragillaria crotonensis,* выращенных при 20^0C, (F) – для культур *Prochlorococcus* MED4, *Phaeodactylum tricornutum* and *Chaetoceros cuvisetus*, выращенных при 23 - 25^0C.

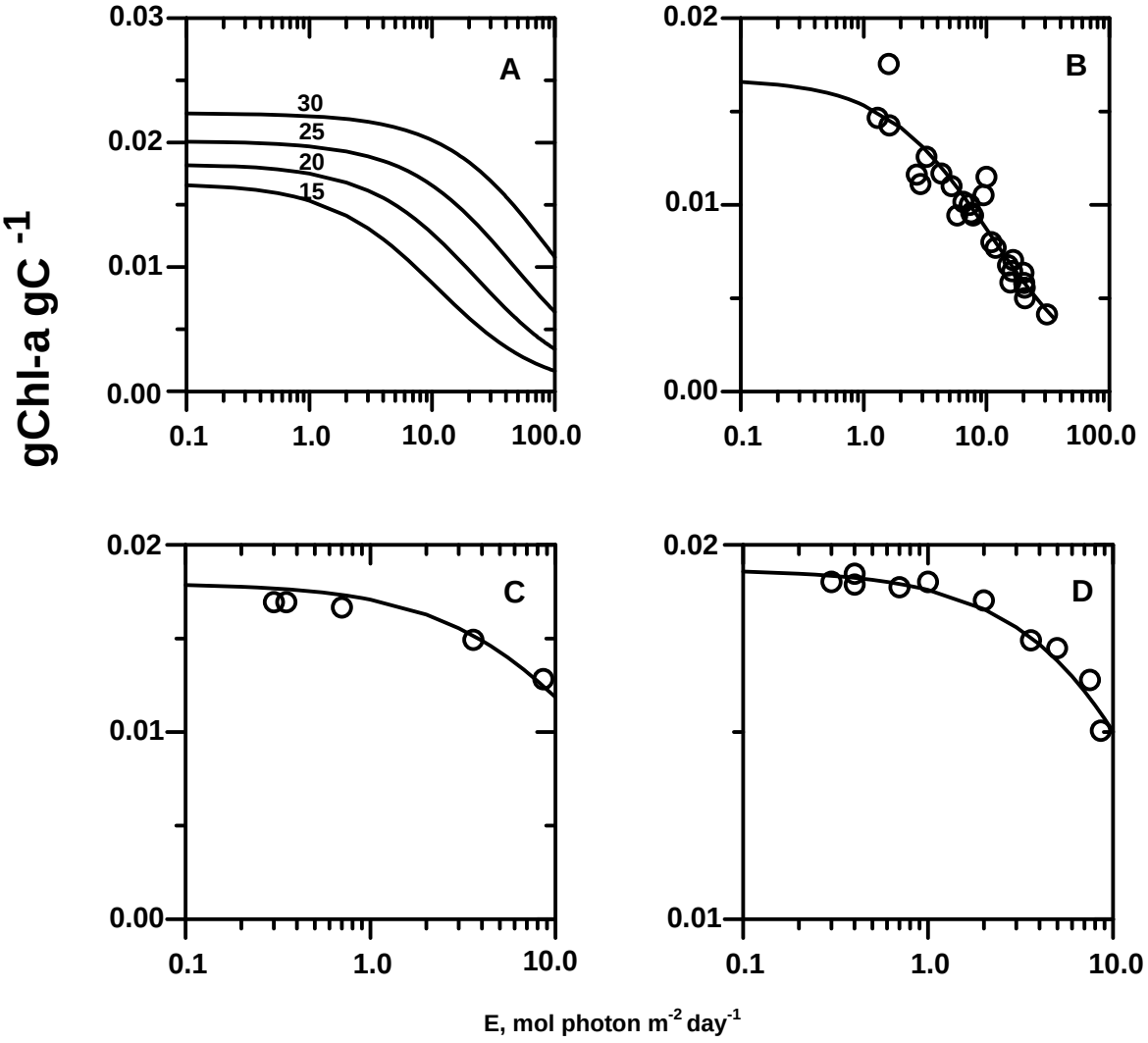

Fig. 4. Comparison of model fits (the solid lines), with observations data (●) for the nutrient-replete cultures of Dinophyceae. (A) - Results of modelling: (B) - *Prorocentrum mariae- lebouriae, Alexandrium excavatum, Gymnodinium galatheanum* grown at 15^0 C, (C) - *Gymnodinium kowalevskii* grown at 19^0 C, (D) - *Exuviaella cordata* and *Peridinium trochoideum* grown at 23 - 25^0 C.

Рис. 4. Сравнение данных модели (сплошные линии) с измеренными данными в культурах Dinophyceae, обеспеченных биогенными элементами. (A) – Результаты моделирования: (B) – культуры *Prorocentrum mariae-lebouriae*, *Alexandrium excavatum, Gymnodinium galatheanum*, выращенные при 15^0C, (C) – культура *Gymnodinium kowalevskii*, выращенная при 19^0C, (D) – культуры *Exuviaella cordata* и *Peridinium trochoideum*, выращенные при 23 - 25^0C.

Table 3. Results of linear regression for the dependence of θ/θ_m on μ/μ_m from published data

Таблица 3. Значения коэффициентов линейной регрессии для зависимости между относительной концентрацией хлорофилла *a* ($\theta/\theta m$) и относительной скоростью роста (μ/μ_m), рассчитанных по литературным данным

Species	Limitation	Irradiance	D	T	n	a	b	r^2	Source
Chlorophyceae									
Dunaliella tertiolecta	NO_3	333	1	25	6	-0.16(0.13)	1.01(0.21)	0.85	[9]
D. tertiolecta	NO_3;NH_4	90	1	18	63	0.20(0.04)	0.75(0.04)	0.98	[41]
D. tertiolecta	NO_3	270	0.5	20	6	0.37(0.18)	0.86(0.15)	0.75	[52]
D. tertiolecta	NO_3	165	1	22	3	0.04(0.10)	0.91(0.20)	0.95	[80]
Bacillariophyceae									
Skeletonema costatum	NO_3	1200	1	15.5	7	-0.03(0.03)	1.04(0.05)	0.99	[75]
S. costatum	NO_3	99.4	1	15.5	6	-0.12(0.07)	1.06(0.10)	0.96	
S. costatum	NO_3	40.5	1	15.5	5	0.18(0.11)	0.82(0.16)	0.82	
S. costatum	NO_3	12	1	15.5	4	0.07(0.13)	1.03(0.30)	0.86	
S. costatum	NO_3	603	0.5	15.5	5	0.11(0.02)	0.89(0.03)	0.99	
S. costatum	NO_3	99.4	0.5	15.5	5	0.18(0.07)	0.86(0.11)	0.95	
S. costatum	NO_3	40.5	0.5	15.5	5	0.18(0.11)	0.82(0.16)	0.89	
S. costatum	NO_3	12	0.5	15.5	4	0.07(0.13)	1.03(0.30)	0.86	
Cyclotella nana	NO_3	333	1	25	8	-0.11(0.14)	1.04(0.19)	0.84	[9]
Thalassiosira pseudonana	NO_3;NH_4	90	1	18	74	0.13(0.03)	0.80(0.03)	0.98	[41]
T. pseudonana	NO_3	240	0.5	20	3	0.23(0.08)	0.78(0.11)	0.96	[21]
T. fluviatilis	NO_3	230-247	0.5	20	5	0.08(0.08)	0.86(0.13)	0.94	[52]
T. allenii	NO_3	270	0.5	20	9	-0.05(0.07)	0.95(0.08)	0.95	
Prymnesiophyceae									
Monochrysis lutheri	*NO_3*	*270*	*0.5*	*20*	*5*	*0.37(0.18)*	*0.86(0.25)*	*0.75*	[52]
M. lutheri	NO_3	330	1	25	5	-0.08(0.16)	0.94(0.26)	0.81	[9]
Pavlova lutheri	NO_3	188	1	22	6	-0.01(0.05)	1.09(0.09)	0.97	[10]
P. lutheri	NO_3	63	1	22	4	0.33(0.08)	0.70(0.17)	0.90	
Isochrysis galbana	NO_3	175	1	18	9	0.14(0.02)	0.84(0.03)	0.99	[45]

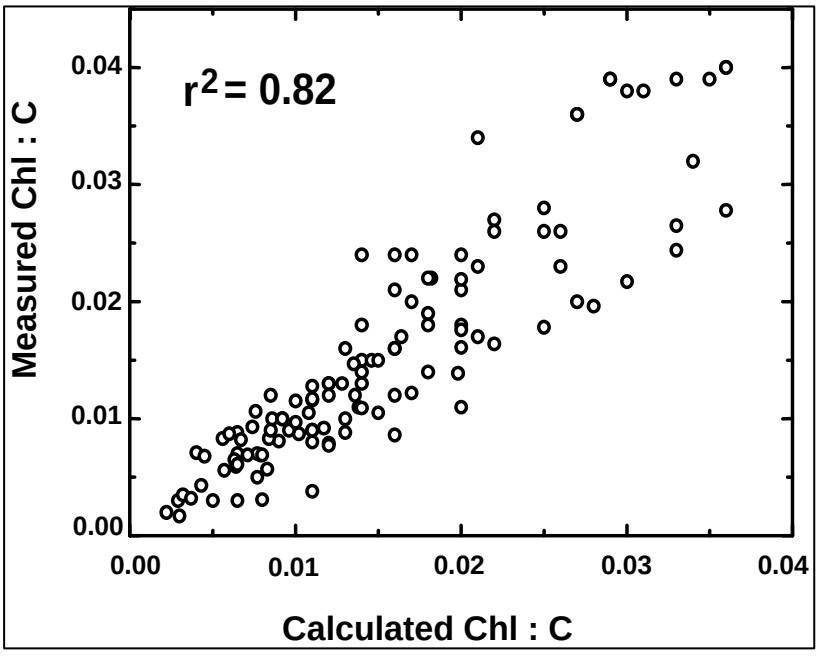

Fig.5. Comparison of the Chl:C ratio obtained from equation (8) with observed data under nutrient-limited conditions for 11 species from 3 taxonomic groups: Chlorophyceae, Bacillariophyceae and Prymnesiophyceae.

Рис. 5. Сравнение Хл:С отношения, рассчитанного по уравнению (8) с данными, измеренными у 11 видов водорослей из трех таксономических групп: Chlorophyceae, Bacillariophyceae, Prymnesiophyceae, лимитированных биогенными элементами.

Data scatter around the regression curve might be explained by a number of reasons, 1) data are obtained in growing cultures in chemostats, 2) there are under-estimated intra-species differences in adaptation rates to irradiance and temperature modes, and 3) parameter measurements have been conducted when algal cultures were in different phases of the light-dark cycle.

In general, the equation derived in (8) does correctly mirror the expected trends of the chlorophyll to carbon ratio for different taxonomic groups in connection with the basic environmental factors. The equation enables the phytoplankton biomass in carbon units to be assessed from the chlorophyll *a* concentration.

Discussion. There are large amounts of published information on the photosynthetic rate and pigment concentration of microalgae. Although numerous it does not allow an estimate to be made of how the chlorophyll *a* concentration varies in different taxonomic groups from similar conditions. In some papers, special attention has been paid to the fact that the chlorophyll content in Bacillariophyceae is higher than in Dinophyceae [11, 27, 33, 34]. Comparison of data for 7 taxonomic groups of algae, obtained under similar conditions, showed that minimum C:Chl ratio increases in following order: Chlorophyceae < Bacillariophyceae; Prochlorococcus < Prymnesiophyceae < Cyanophyceae < Dinophyceae. The data obtained under low irradiance in 5 Chlorophyceae species [23, 77], some strains of *Synechococcus* [43, 82] and *Prochlorococcus* [7], which have not being included in Table 1, confirm this regularity. The results of a study of some other species were not consistent with experimental data from Table 1 and have not been used in the analysis.

Thompson et al. [88] obtained extremely high C:Chl ratios at 17.5°C in 5 Bacillariophyceae species. Our calculation demonstrated that θ^{-1}_{max} ranged from 47 to 75 gC gChl a^{-1} and was from 99 to 346 gC gChl a^{-1} under light intensity 225 μE m^{-2} s^{-1}, these are as much as 2 to 3 times different from data obtained for the same species by other authors (Table 1). In another paper on the same species under similar conditions (T = 20°C and E = 220 μE m^{-2} s^{-1}) the C:Chl-ratio was lower by 35 to 75 gC gChl a^{-1} [89]. The authors do not give any information to explain these differences. One can assume the contradictions are due to peculiarities of the cultivation method or experimental procedure.

Data on *Prorocentrum micans* at low growth rate [24] have not been analysed within the Dinophyceae group, because θ^{-1} was much higher than the mean value for the Dinophyceae. In *P. minimum,* at rather high growth rate, the C:Chl ratio was close to the mean value for this group [47]. The reasons for this discrepancy could be many but it can not be excluded they depend upon a microalgae growth rate under similar conditions. In *Gyrodinium aureolum* and *Gymnodinium galatheanum* θ^{-1}_{max} ranged from 30 to 60 gC gChl a^{-1} at 15° C [47, 66, 67,]. The minimum values are close to those in the Bacillariophyceae. Probably, not all the species in this group are characterised by higher values of the C:Chl ratio compared to the Bacillariophyceae. The extreme values within the same taxonomic group vary no more than twice.

Geider [33] examined the combined effects of irradiance and temperature on the C:Chl ratio in 13 species of algae from 3 taxonomic groups. He computed θ^{-1}_{max} and β coefficients ac-

cording to equation (2) and found the first one changes linearly as temperature increases and the latter changes exponentially.

New experimental data obtained during the last few years verifies the temperature-dependent types of β and θ^{-1}_{max}. Numerical parameters of Geider's [33] and our equations are slightly different, because they are obtained for different number of species. However, in case of *Microcystis aeruginosa* cultivated at 29° C Geider made a mistake in the computation of θ^{-1}_{max} and β. According to the author, θ^{-1}_{max} and β are 6.4 and 0.038. From experimental data of Raps et al. [72] these values are given as 59.5 gC gChl a^{-1} and 0.39 gC gChl a^{-1} m^{-2} μE s^{-1}.

Cloern et al. [14] described the combined effect of light, temperature and nutrients on C:Chl ratio in the equation:

$$\theta = 0.003 + 0.0154 \exp(0.05\ T)\exp(-0.059\ E)\mu^* \quad (9)$$

where E is mol quanta m^{-2} d^{-1}, μ^* is the relative growth rate limited by nitrogen (μ/μ_{max}, where μ_{max} is the growth rate in replete nutrients conditions at light E and temperature T). The model does not imply that the chlorophyll to carbon ratio differs between taxonomic groups. Experimental data for 16 phytoplankton species from 4 taxonomic groups, which were grown at temperatures from 0^0 C to 25^0 C at E< 30 mol photon $^{-1}$ day^{-1}, obtained from the literature were taken as the basis of our calculations. In general, the calculated values are in fairly good agreement with the measured ones (r = 0.78). However, our calculations made for 36 species of 7 taxonomic groups (Table 1) at $\mu^* = 1$ show that equation (9) explains only 44 % of the Chl:C ratio variability (Fig. 6).

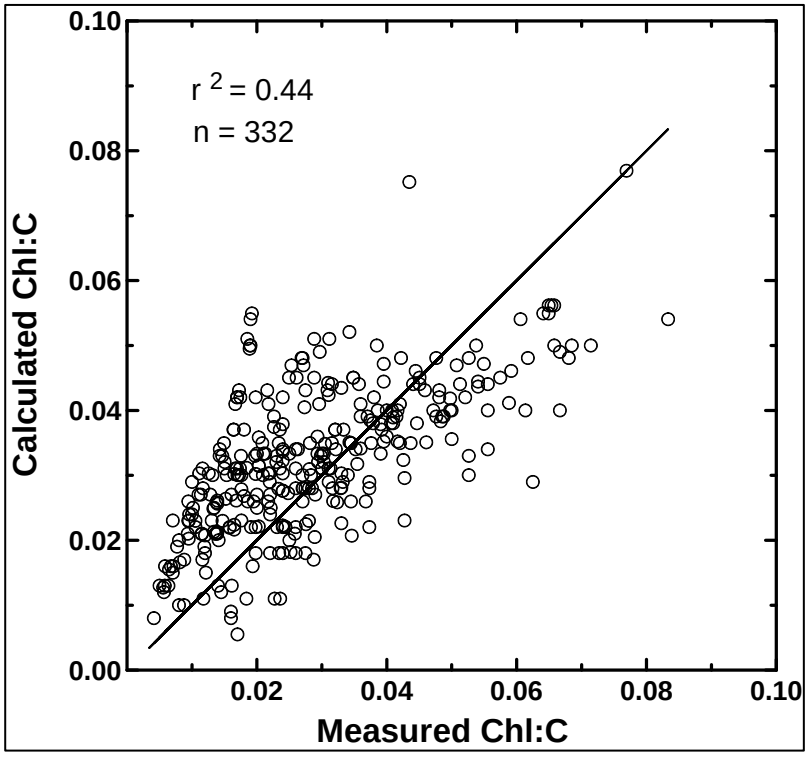

Fig. 6. Comparison computed Chl:C ratio from equation (9), with observations for nutrient-replete cultures (Table 1). The line shows a 1 : 1 relation.

Рис. 6. Сравнение Хл:С отношения, рассчитанного по уравнению (9) с измеренными в культурах, обеспеченными биогенными элементами. Линия показывает отношение 1:1.

The difference between computed estimates and those from experiments is pronounced, especially with regard to the low values. The explanation lies in that the model over estimates the Chl:C ratio for Dinophyceae and Cyanophyceae as much as 2 times compared to actual measurements; although it is lower in other varieties of phytoplankton. On the whole, our equations are more efficient at predicting changes in chlorophyll to carbon ratio generated by the combined effect of light, temperature and nutrients (Figs. 2 and 6) in comparison with the model proposed in Cloern et al. [14].

There are no convincing data published on the combined effects of light and temperature on the chlorophyll content of phytoplankton. There are only 2 experiments with 2 algae species where contradictory results were obtained [90, 93]. In *Skeletonema costatum* within the temperature range 0° to 22°C the C:Chl ratio was practically constant while in *Leptocylindricus* it increased regularly as temperature decreased and β-coefficient increased as temperature declined. Observations on *S. costatum* show θ^{-1}_{max} is 34 ± 3.9 gC gChl a^{-1} on average in the temperature range 0° to 22° C. A similar value was obtained at -0.5° C in 3 diatoms isolated from the Barents Sea plankton [44]. Experiments in the temperature range -1.6° to 12° C and under low light intensity (E = 25 mol quanta m^{-2} s^{-1}) have not demonstrated regular change of the C:Chl ratio in *Nitzschia seriata* [79]. The mechanism of temperature adaptation of phytoplankton under low light intensity is still not fully understood and there are reasons to believe that an increase of θ^{-1}_{max} is not always associated with a decrease of temperature. According to our results, the C:Chl ratio must decrease as temperature increases under high light intensity in all phytoplankton species. This tendency was found in 8 species from 3 taxonomic groups cultivated under the same irradiance, 220 μE m^{-2} s^{-1} within temperature ranges from 10° to 25° C [89]. Between 15° and 25°C the C:Chl ratio decreased by 2.2 times and values were in good agreement with those calculated from equation (6). It is important to note two features of the equations (Table 2). The first is the temperature effect on the decrease of the C:Chl ratio when the light intensity declined. The second the relative chlorophyll *a* content of cell, which under different irradiance depends on its maximum at E ≈ 0 and the daily light density flux. It varies proportionally with the quantity of energy and does not depend on the light period. Confirmation of this thesis can be obtained from the experimental data for *Skeletonema costatum* where the light-dark cycle varied from 2 L : 22 D to 24 L : 0 D and irradiance was from 12 to 2000 μE m^{-2} s^{-1} [74, 75].

The dynamic model of phytoplankton photo-adaptation was developed [38, 39] on the basis of matter and energy balance in the cell and the correlation between the Chl:C ratio, growth, photosynthesis and respiration rates [28, 37, 50, 53]. The effects of light intensity on the Chl:C ratio can be described with 3 parameters:

$$\theta = \theta_{max} / 1 + (\theta_{max}\, \alpha_{chl}\, E / 2\, P_m) \qquad (10)$$

where P_m is the maximum photosynthesis rate normalised by carbon, s^{-1}, α_{chl} is the slope of the light-photosynthesis curve, gC gChl a^{-1} m^2 μmol^{-1}photons; θ_{max} is the maximum Chl:C ratio, gChl *a* gC^{-1}; E is irradiance, μmol photons $m^{-2}s^{-1}$.

Analysing the equation system from Geider et al. [39]:

$$P_m / \alpha_{chl}\, \theta_{max} = \theta^{-1}_{max} / 2\, \beta \qquad (11)$$

where θ^{-1}_{max} and β are the coefficients of equation (2). If $\theta^{-1}_{max} / 2\beta$ is represented as K from equation (11) then:

$$\theta = \theta_{max} / (1 + E / 2 K) \qquad (12)$$

where K is the saturation parameter for the growth-irradiance curve, μmol photon m^{-2} s^{-1}[39].

This equation is produced on the assumption that photosynthetic efficiency and P_m are light independent and chlorophyll *a* biosynthesis is in proportion to P_m. Computed from equation (6), the coefficient K increases regularly in the temperature range from 0 to 30° C (Fig. 7).

It can be observed from Fig. 7 that given the same temperature (e.g. 20° C) diatoms develop light saturation at the irradiation 4.4, Dinophyceae - 11.4 mol photon m^{-2} day^{-1} and the remainder of phytoplankton at intermediate values of irradiation. The coefficient K, calculated using three parameters ($K = Pm / \alpha \theta_{max}$), measured in 15 species of algae, which were cultivated at a series of temperatures [39] yields very similar estimates (Fig. 7). The Chl:C ratios computed from equations (6) and (12) for a variety of temperature and irradiance values are identical. Under low light intensity the Chl:C ratio increases 1.2 to 1.6 fold with a temperature rise of 10° C and under high light intensity it increases about 3 to 4 fold.

From our results, four parameters should be known to estimate the C:Chl ratio for *in situ* phytoplankton populations: 1) biomass values of individual microalgae groups; 2) the extent to which phytoplankton growth rate is limited by nutrients; 3) the light flux density at depth; and 4) temperature. We shall take the results of a study conducted in oligo-, meso-, and eutrophic regions of the tropical Atlantic Ocean in the EUMELI programme (June, 1992) as an example for calculation.

Biomass relations. In this study the numbers of microalgae were counted with a flow cytometer [69]. The prokaryotes, *Synechococcus* and *Prochlorococcus* were abundant in the 0 to 100 m layer, they approximated 96 to 99 % of total number algae in oligo- and mesotrophic regions and 75 % in eutrophic ones. To calculate biomass it is assumed that *Prochlorococcus* contains 53 fgC $cell^{-1}$, *Synechococcus* 250 fgC $cell^{-1}$ and the picoeukaryotes 2100 fgC $cell^{-1}$ [69]. From the abundance values and carbon content in cells the biomass relationship of *Synechococcus: Prochlorococcus*: Picoeukaryotes, in the 0 to 100 m layer was determined and averaged. These were 0.5 : 6.0 : 3.5 in oligo- and 7.1 : 0.1 : 2.8 in mesotrophic sites respectively. The taxonomy of the eukaryotes has not been fully studied and we assume that Bacillariophyceae, Prymnesiophyceae and Dinophyceae appeared to be in the same proportion. In the eutrophic waters the diatoms ranged up to 88 % of the phytoplankton biomass.

Based on biomass relations of individual taxonomic groups the mean weighting θ^{-1} was computed for particular temperature conditions within the photosynthetic zone.

Limitation of phytoplankton growth rate by nutrients. The phytoplankton assimilation rate of inorganic nitrogen was not measured in this study. Results on kinetics of its consumption in the subtropical Atlantic were used [42]. In near shore and offshore areas a clear dependence was found: K_N the value (for nitrate and ammonium) increased in proportion to its concentration in the water. The value of K_N for nitrate and ammonium in coastal phytoplankton communities is usually over 1 μM while in oceanic communities it ranges from 0.02 to 0.03 μM.

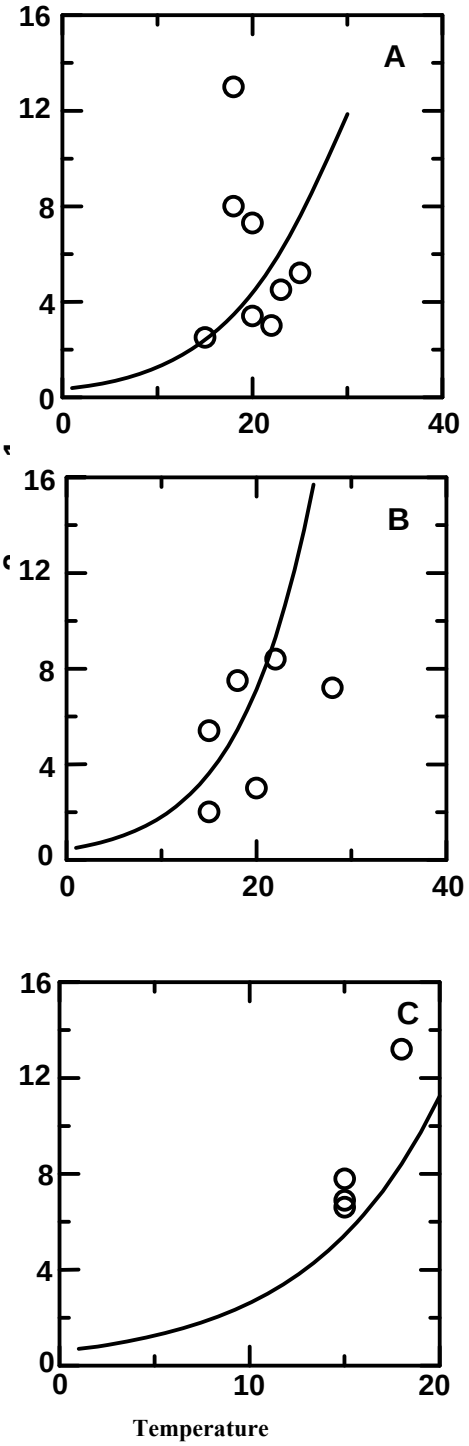

Fig. 7. Influence of temperature on the saturation parameter for the growth rate-irradiance curve, mol photon m^{-2} day^{-1} (K). The line is the fitted value of θ_{max}^{-1} / 2β (θ_{max}^{-1} - measured from equation 4, β - measured from equation 5). Variation of model predictions (O) of the K parameter (P_m/α_{chl} θ_{max}) as a function of temperature for nutrient-replete cultures. (A) – for Bacillariophyceae, (B) – Chrysophyceae, Cyanophyceae, Prymnesiophyceae, (C) – Dinophyceae.

Рис. 7. Влияние температуры на параметр светового насыщения кривой скорость роста – свет, моль фотон $м^{-2}$ $сут^{-1}$ (К). Линия соответствует отношению $\theta_{max}^{-1}/2\beta$ (θ_{max}^{-1} - рассчитано по (4), β - по (5). Изменение парамет-ра К по модели (P_m/α_{chl} θ_{max}) как функции температуры в культурах, обеспеченных биогенными элементами (О). (А) – Bacillariophyceae, (В) – Chrysophyceae, Cyanophyceae, Prymnesiophyceae, (С) – Dinophyceae.

Studies conducted within the framework of EUMELI programme estimated the content of nitrates in surface water of oligo-, meso- and eutrophic areas as 0.01, 0.5 and 11.0 μM respectively. Given these nitrogen contents and K_N estimates, the ratio between the rate of nitrogen consumption in near surface phytoplankton (V) and maximum rate (V / V_{max}), possible in oligo-, meso- and eutrophic water, is 0.3, 0.5 and 1.0 respectively. At steady state, the nutrient consumption rate of microalgae becomes proportional to their growth rate; when $K_N \approx K\mu$. From experiments performed on several species of diatoms, it was seen that the half-saturation constants obtained for the growth and consumption of nutrients were very similar [20].

However, these empirical results are not in perfect agreement with theoretical deductions and recent experiments [62]; $K_N \approx K\mu$ was maintained provided that the store of nutrients in the cell (Q) remained relatively unchanged. When phytoplankton growth rate is considerably limited by nitrogen ($\mu_{max} / \mu = 10$), then $Q_{max} / Q_o = 2$ to 3, where Q_o is the minimum content of intracellular nitrogen at $\mu = 0$. According to Morel [62], K_N can be 4 to 9 times greater than K_μ. These pronounced differences between intracellular nitrogen estimates are seen during short incubations (minutes) when membrane transport processes prevail as nutrients are added. During longer incubations (hours) macromolecular synthesis dominates and cells gradually develop a new steady state [92]. Given the same difference in the content of intracellular nitrogen, the K_N to K_μ ratio equals 2 - 3.

It was stated by Harrison et al. [42] that the intracellular nitrogen content, in incubations of 3 hours, can not vary several times. A proof to this hypothesis can be seen in the following computations. In oceanic communities of phytoplankton with chlorophyll *a* content of 0.05 - 0.1 μg / l the maximum ammonium assimilation rate is 4 to 6 nM hr^{-1}. Assuming a particular time span with $\mu = 0$, and with the C:Chl and C : N ratios estimated as 150 and 15 respectively, then the content of intracellular nitrogen will not change by more than 25%. With $\mu > 0$ the difference is even less. If Q varies like that over the incubation time, then K_N may be 25% higher on average as K_μ. The accuracy of the K_N estimation is about ± 10% [42], therefore we assumed $K_N \approx K_\mu$ in our calculations.

Light flow densities within the water column and the phodoadaptive state of phytoplankton. The chlorophyll *a* to carbon ratio and the chlorophyll *a*–specific light-saturated photosynthesis rate (P^B_{max}) are two of the most widely used indices the photoadaptive state of phytoplankton [38]. Natural variability of the P^B_{max} was studied in the EUMELI programme at three sites in the Northeast tropical Atlantic representing typical eutrophic, mesotrophic and oligotrophic waters [1]. At the eutrophic and mesotrophic sites, where the mixed layer extended deeper than the euphotic layer, P^B_{max} was constant with depth. At the oligotrophic site the mixed layer depth averaged about 70m. From the top to the bottom in the mixed layer, P^B_{max} decreased slightly (< 25%). At all 3 sites there was not a progressive vertical change in the P^B_{max} within the mixed layer it would be expected that within the mixed layer phytoplankton is acclimated to mean light flow density. It can be calculated from (1) as

$$E_{ml} = E_o[(1 - \exp(-4.5Z_{ml}/Ze)] / 4.6Z_{ml}/Ze) \quad (13)$$

where E_o is the light flow density (PAR) incident to surface, E m^{-2} d^{-1} and Z_{ml} and Ze are depths of the mixed layer and photosynthesis zone respectively. Within the stratified layer phytoplankton appears to be adapted to the irradiance, which is available at fixed depths:

$$E_z = E_o \exp(-kz), \quad (14)$$

where k is the attenuation coefficient of light (PAR).

Temperature. Measurements were taken in June in the mixed layer and throughout the photosynthetic zone. Maximum C:Chl ratios of 96 to145 gC gChl a^{-1} were observed within the mixed layer, which gradually decreased with depth to 30 gC gChl a^{-1} in the oligotrophic site (Table 4).

Table 4. The ratio of phytoplankton carbon to chlorophyll *a* in oligotrophic, mesotrophic and eutrophic situations (Calculated from EUMELI programme)
Таблица 4. Соотношение углерода в фитопланктоне к хлорофиллу *a* в олиготрофных, мезотрофных и эвтрофных ситуациях (рассчитано по данным программы EUMELI)

Depth, m	E, mol m^{-2} d^{-1}	T, °C	gC gChl a^{-1}	μ / μ_{max}	Z_{mix} , m	Ze , m	%, of total biomass		
							Pr.	Syn.	Euk.
Oligotrophic site									
0-50	22	25	145	0.3	50	110	61	5	34
60	4.0	24	40	0.75					
70	2.6	23	33	1.0					
80	1.7	20	33	1.0					
90	1.1	20	32	1.0					
110	0.5	20	31	1.0					
125	0.2	19	30	1.0					
Mesotrophic site									
0-45	6	24	96	0.5	45	25	10	71	28
Eutrophic site									
0-48	4	18	37	1.0	48	17	5	7	88

In all sites E_0 equal 50 mol m^{-2} d^{-1}.

In the eutrophic sites the C:Chl ratio averaged 37 within the mixed layer. Phytoplankton adaptation to environmental conditions results in the C: Chl ratio in the surface waters varying within narrow limits.

The mean weighting integral value of C:Chl ratio into photosynthetic layer in oligotrophic waters was 78, in mesotrophic ones it was 96. The calculated values do not strongly diverge from the data obtained on chlorophyll concentration and phytoplankton biomass in June 1992 in EUMELI programme. In this period the sum of chlorophyll *a* and divinyl-chl *a* in oligo- and mesotrophic waters waters was 34.6 and 55.8 mg m^{-2} and phytoplankton biomass measured with the flow cytometer on cell abundance and carbon content in the cell were 2.0 and 4.7 gC $^{-2}$ accordingly [69]. The comparison of these values results in C:Chl ratio in oligotrophic waters is 58, in mesotrophic ones is 84.

Similar values were obtained in earlier studies where a comparison of the chlorophyll concentration and phytoplankton biomass, measured on the basis of photosynthesis rate kinetics during the day, was made [19, 29]. From the results of these investigations the C:Chl ratio in nutrient rich areas averaged 33 while in nutrient depleted ones was 100. Vertical distribution of phytoplankton biomass in terms of carbon content and its relationship with chlorophyll *a* concentration were examined in the tropical and subtropical western Pacific Ocean [32]. Fluorescence microscopy combined with image analysis was used for measurement of cell volume, which was converted to phytoplankton carbon. The C:Chl ratio decreased with depth of 93 ± 44 to 52 ± 15. The ^{14}C-chlorophyll *a* labelling technique was used to estimate C:Chl ratios of phytoplankton in Dabob Bay, Washington [91]. They observed vertical variability with maximum value (150) at the surface in August when irradiance was greatest and minimum values (20 - 35) at depth. Total carbon biomass of phytoplankton was estimated using a combination of flow cytometry with literature

values of cell carbon contents in the tropical Pacific representing typical oligotrophic regime [8]. In nutrient depleted tropical waters the C:Chl ratio within the mixed layer was 128 and decreased to 25 - 50 at deeper depths. Using the same approach as Campbell et al., Li et al. [57] and Buck et al. [6] presented different data for the oceanic areas of the tropical and subtropical Atlantic Ocean. From Li et al. the C:Chl ratio within the mixed layer was 44 and declined to 15 with depth; the values from Buck et al. for surface were 172 ± 51 and 180 ± 39 for tropical and subtropical regions respectively. Theoretically such discrepancies are possible if phytoplankton in one situation is not limited by nutrients while in another it is severely limited. We presume that the reason is the various biomass relationships of *Synechococcus*: *Prochlorococcus*: eukaryotes which were 1 : 2 : 4 in Li et al. [57] and 1 : 6 : 3 in Buck et al. [6]. This may have arisen from an underestimation of the biomass of *Prochlorococcus* in the former and a wrong estimation of organic carbon content in the latter. Our model predicts a pattern of C:Chl that is broadly consistent with the observations [6, 8, 69, 91].

A description of acclimation of the growth rate and C:Chl of phytoplankton to irradiance, nitrate concentration and temperature by Geider et al.[39] was incorporated into model of phytoplankton production dynamics [85]. The model predicts that changes in concentration of chlorophyll a will be accompanied by substantial vertical and temporal variations in the C:Chl in the North Atlantic. During the summer the C:Chl ratios were ranged from 25 to 160 between equator and 35^0N. Highest values were predicted for the nutrient- depleted surface mixed layer. Lowest values were predicted for the top of the nutricline within the seasonal thermocline. The range of values predicted by the model Taylor and coworkers compares favourably with our model predictions. The regulation of C:Chl in both models is qualitatively similar. However, the Taylor et al. model require knowledge of maximum carbon-specific rate of photosynthesis (P^C_{max}) and maximum Chl:C ratio in order to specify the dynamics of physiological acclimation The model does not imply that the chlorophyll to carbon ratio and P^C_{max} differs between taxonomic groups.

Our steady-state model does not resolve variations of C:Chl ratio that may occur with time of day. In the sea, phytoplankton may experience large variations in incident irradiance on time scales of hours to days. Turbulence in the upper mixing layer of the ocean transports algal cells through a light field fluctuates that decreases exponentially from the sea surface and a major source of variability in physiological performance of phytoplankton may be due with Langmuir circulation or turbulent mixing [49, 58]. The photoacclimation responses of phytoplankton depend on the relation between the time scale for the vertical mixing and time scale for photoresponsive parameters [18, 55]. The model predicts that at high of rates of turbulent kinetic energy dissipation, ε, [2 - 12ε (m^2 s^{-3}) × 10^7], little depth variation in P^B_{max} and P (pg-at. O_2 h^{-1} $cell^{-1}$) was observed; when energy dissipation rates were low [<2ε (m^2 s^{-3}) × 10^7], the difference between surface samples and those at the base of the mixing a non-linear decrease [31, 55]. However, there are difficulties in direct measurements of light energy that is available to phytoplankton in the photic zone, which changes on several time-scales. First order variations of light energy are associated with diurnal path of the sun and meteorological conditions. Second order variations are regulated

by such factors as surface waves, Langmuir circulation, and cellular motility. These time-scales produce for the phytoplankton a complex the irradiance flux density that varies of seconds to days. Phodoadaptation, involving the regulation of C:Chl ratio have the longer time scales of hours to days [18]. Direct comparisons of phytoplankton organic carbon with chlorophyll *a* concentration show small degree variability of C:Chl in the upper mixed layer [8, 32, 57, 59], although light-saturated photosynthesis rate (P^{B}_{max}) may decreased from the top to the bottom in the mixed layer [4, 59, 61, 76]. The data are obtained in the Atlantic Ocean indicate that the latitudinal variations in surface P^{B}_{max} did not result from changes in cellular chlorophyll *a* content, but cold have been due to nutrient-induced differences in the turnover time of the photosynthetic units [59].

The results obtained from this study demonstrates that at our present state of knowledge and methods it is possible to use developed equations to estimate relative chlorophyll content in phytoplankton under various conditions.

Acknowledgements: This work was part of the international co-operation program between IBSS and PML and was partly funded by NASA grant N^{o} NAG 5-3113 and the "Darwin Initiative" (UK) N^{o} 162/8/251.

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