Modelled quantum yields and energy efficiency of fluorescence, photosynthesis and heat production by phytoplankton in the World Ocean*

doi:10.5697/oc.54-4.565
OCEANOLOGIA, 54 (4), 2012.
pp. 565–610.

KEYWORDS
World Ocean
Sun-Induced Chlorophyll *a* Fluorescence (SICF)
Photosynthesis
Heat production by phytoplankton
Utilization budgets of the excitation energy of pigment molecules
Quantum yields and energy efficiences of chlorophyll *a* fluorescence
Photochemical, and non-photochemical quenching of fluorescence

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Received 21 August 2012, revised 27 September 2012, accepted 5 October 2012.

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* Support for this study was provided by the project Satellite Monitoring of the Baltic Sea Environment – SatBałtyk funded by the European Union through European Regional Development Fund contract No. POIG 01.01.02-22-011/09.

The complete text of the paper is available at http://www.iopan.gda.pl/oceanologia/

Abstract

The paper discusses the utilization budgets of the excitation energy of phytoplankton pigment molecules activated on absorbing solar radiation under various typical conditions obtaining in the World Ocean. The deactivation of these molecules following the conversion of the excitation energy to the fluorescence of chlorophyll *a*, the photosynthesis of organic matter and heat is taken into account. To this end, a great many model computations were performed; these made use of the authors' earlier models of the dependence of the quantum yields and energy efficiencies of the above processes on the three principal environmental factors governing the functioning of marine plant communities: the chlorophyll *a* concentration in the surface water layer (the trophic index of waters), temperature and the underwater irradiance at different depths in the sea. These model relationships were used to determine vertical profiles of the quantum yields and energy efficiencies of the chlorophyll *a* fluorescence, photosynthesis and heat production by phytoplankton in different trophic types of sea in three different climatic zones (tropical, temperate and polar), in two seasons of the year – June (summer in the northern hemisphere) and January (winter in the northern hemisphere). The results of the calculations are given for areas of oceanic Case 1 waters, which cover more than 90% of the volume of all basins in the World Ocean (according to the optical classification by Morel & Prieur 1977). The results of these calculations, though preliminary, provide a comprehensive description of the range of variability of the yields/efficiencies of the three deactivation processes. The results have made it possible to summarize, within the context of the euphotic zone, of the budgets of phytoplankton pigment molecule excitation energy expended on three complementary processes, namely, the fluorescence of chlorophyll *a*, the photochemical assimilation of inorganic carbon and the photosynthesis of organic matter, and the radiationless, nonphotochemical conversion of the pigment molecules' activation energy to heat.

1. Introduction

1.1. The objective of the model studies

One of the most important processes sustaining life on Earth is the photosynthesis of organic matter and the liberation of oxygen in plant cells. The phytoplankton of seas and oceans make up the vast majority of these cells. The photosynthetic primary production of phytoplankton is the first link in the trophic chain of marine organisms, which supplies marine ecosystems with energy and controls the inflow of this energy (Steemann Nielsen 1975, Lieth & Whittaker 1975, Kowda 1976, Falkowski 1980, Kirk 1994, Woźniak et al. 2003). Marine phytoplankton is also one of the main regulators of the balance between oxygen and carbon dioxide in nature (e.g. Glantz 1988, Kellog 1988, Trenbertch 1992, Kożuchowski & Przybylak 1995, Michael et al. 2006, Armbrust 2009). It therefore influences the greenhouse effect in the Earth's atmosphere and hence the planet's climate.

In view of the transformations of the global climate and living environment, and the significant part played by marine photosynthesis in them, many oceanographic centres around the world are striving to acquire a more accurate knowledge of the environmental conditions governing the intensity of photosynthesis and are attempting to predict the effects of its changes on the aforementioned transformations.

Phytoplankton cells draw the energy to drive photosynthesis from the sunlight entering the sea water. The quanta of this light are selectively absorbed by the various pigments contained in these cells. However, only part of the energy activating the pigment molecules as a result of light absorption is expended during photosynthesis; the remainder is deactivated in two other processes, namely, fluorescence, and radiationless nonphotochemical quenching, which generates heat (Butler & Kitajima 1975, Weis & Berry 1987, Kolber & Falkowski 1993, Ostrowska 2001). The objective of the present work is to investigate and model the distribution of the activation energy of phytoplankton pigment molecules among these three processes under the many and various conditions prevailing in the marine environment. Photosynthesis itself is, of course, the most important of the three processes, its yield being governed by environmental factors determining their utilization of this energy. Our models describe the distribution of this energy by comparing the quantum yields and energy efficiencies of the three processes. These yields/efficiencies are complex functions of environmental state parameters. Our models take these relationships into account and enable the distribution of the pigment excitation energy to be calculated for the various typical conditions obtaining in the waters of the World Ocean.

1.2. Presentation of the physical problem; definitions of the process yields

The light-absorbing pigments in phytoplankton cells can be classified into two groups. One comprises the photosynthetic pigments, PSPs (the main abbreviations and symbols used in the text are listed in Annex 1), contains chlorophyll *a* and a set of pigments accessory to chlorophyll *a*. These accessory pigments absorb light from different spectral bands, and the energy thereby acquired drives the processes contributing to the photosynthesis of organic matter. Plant cells form PSPs in order to make optimal use of the light spectrum available in their particular living environment. The other group consists of photoprotecting pigments (PPPs), which protect chlorophyll *a* at the photosynthetic reaction centres from an undesirable excess of light energy (e.g. Bartley & Scolnik 1995, Majchrowski 2001, Pascal et al. 2005, Woźniak & Dera 2007). Figure 1 shows in

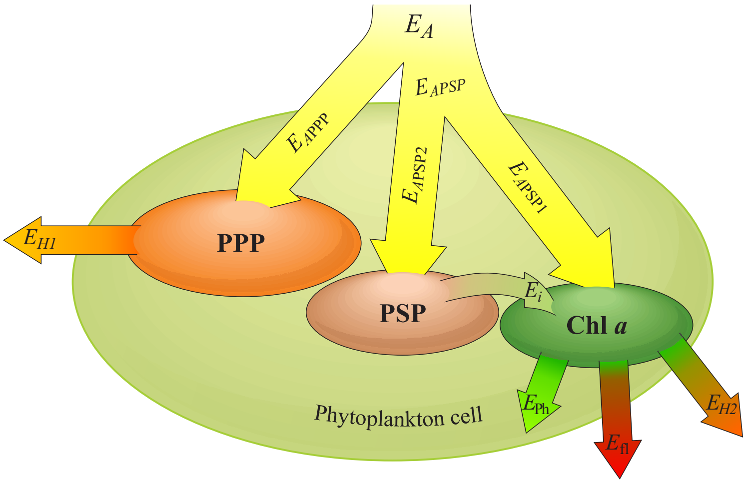

Figure 1. Transfer and distribution of absorbed light energy in a phytoplankton cell. E_{APPP} – energy absorbed by photoprotecting pigment molecules (PPPs). E_{APSP} – energy absorbed by photosynthetic (E_{APSP1} – by chlorophyll *a*, E_{APSP2} – by accessory photosynthetic pigments) pigment molecules (PSPs); $E_{\mathrm{APSP}} \approx E_{\mathrm{APSP1}} + E_{\mathrm{APSP2}}$. $E_A \approx E_{\mathrm{APPP}} + E_{\mathrm{APSP}}$ – total energy absorbed by phytoplankton pigments. E_{H1} – energy of activated PPP molecules converted into heat. E_{H2} – part of the excitation energy of chlorophyll *a* molecules converted into heat; $E_H \approx E_{H1} + E_{H2}$ – total energy converted into heat. E_i – internal transfer of PSP excitation energy to chlorophyll *a* molecules. E_{fl} – part of the excitation energy of chlorophyll molecules emitted as fluorescence in the spectral band ca 685 nm. E_{ph} – part of the excitation energy of chlorophyll *a* molecules converted into chemical energy by photosynthesis

a simplified way how these pigments absorb this energy and how it is distributed among the various processes.

Excited PPP molecules are mainly deactivated as a result of radiationless transitions, during which they release their excitation energy E_{APPP} to the surroundings in the form of heat E_{H1}. In contrast, the excitation energy of PSPs E_{APSP}, both that acquired by the direct absorption of light by chlorophyll *a* E_{APSP1}, as well as that obtained by the absorption of light (from various other spectral intervals) by photosynthetic accessory pigments and transferred almost entirely within the cell in a radiationless manner to the chlorophyll *a* molecules at the photosynthetic reaction centres $E_i \approx E_{\mathrm{APSP2}}$, comprises the entire excitation energy of chlorophyll *a* molecules (Butler & Kitajima 1975, Steemann Nielsen 1975, Govindjee 1975, Falkowski 1980, Weis & Berry 1987, Kolber & Falkowski 1993, Ostrowska 2001, Ke 2003). Only a certain part of this energy (E_{ph}) is used in photosynthesis for the assimilation of inorganic forms of carbon, the production of organic matter and the release of oxygen. The unused remainder is liberated in the form of chlorophyll a fluorescence E_{fl} in the spectral band around 685 nm, or is deactivated in a radiationless manner (via internal radiationless conversion of this energy and internal transfer, i.e. excitation of molecules in collisions with other molecules) and released in the form of heat E_{H2}, in the same way as the heat E_{H1} emitted by PPPs.

We assume that the excitation energy of accessory PSP molecules is practically all transferred to chlorophyll a molecules, i.e. $E_{A\mathrm{PSP}2} \approx E_i$, and that this energy E_i, together with the light energy absorbed directly by chlorophyll a, i.e. $E_{A\mathrm{PSP}1}$, is consumed in its entirety by these molecules during the aforementioned three processes. Mathematically we can express this as $E_{A\mathrm{PSP}1} + E_i \approx E_{\mathrm{fl}} + E_{\mathrm{ph}} + E_{H2}$. We apply the same relations to the number of quanta driving these processes (on Figure 1 we replace the quantity of energy E by the number of quanta N): $N_{A\mathrm{PSP}2} \approx N_i$ and $N_{A\mathrm{PSP}1} + N_i \approx N_{\mathrm{fl}} + N_{\mathrm{ph}} + N_{H2}$.

The three processes by which the excited states of phytoplankton pigment molecules are deactivated can be analysed and described in two ways: we can examine the **quantum yield** of these processes or alternatively, we can look at the **energy efficiency** of the processes. Again, we can take two different approaches to investigate the quantum yields (denoted by Φ or q) and the energy efficiencies (R or r) of these processes:

1. Yield/efficiency in the general, broader sense: the quantum yield Φ as the number of quanta or, the energy efficiency R as the amount of energy expended on a given process in relation to the number of quanta or to the amount of light energy absorbed by all phytoplankton pigments, that is, by both PSPs and PPPs ($N_A \approx N_{A\mathrm{PSP}} + N_{A\mathrm{PPP}}$ and $E_A \approx E_{A\mathrm{PSP}} + E_{A\mathrm{PPP}}$ respectively):

   - Energy efficiency of chlorophyll a fluorescence
   $$R_{\mathrm{fl}} = E_{\mathrm{fl}}/E_A. \tag{1}$$
   - Quantum yield of chlorophyll a fluorescence
   $$\Phi_{\mathrm{fl}} = N_{\mathrm{fl}}/N_A. \tag{2}$$
   - Energy efficiency of the photosynthesis of organic matter
   $$R_{\mathrm{ph}} = E_{\mathrm{ph}}/E_A. \tag{3}$$
   - Quantum yield of the photosynthesis of organic matter
   $$\Phi_{\mathrm{ph}} = N_{\mathrm{ph}}/N_A. \tag{4}$$
   - Energy efficiency of the radiationless conversion of the excitation energy of all pigment (PSP and PPP) molecules into heat
   $$R_H = E_H/E_A, \tag{5}$$

where $E_H = E_{H1} + E_{H2}$.

- Quantum yield of the radiationless conversion of the excitation energy of all pigment (PSP and PPP) molecules into heat

$$\Phi_H = N_H/N_A, \tag{6}$$

where $N_H = N_{H1} + N_{H2}$.

2. Yield/efficiency in the stricter, narrower sense: the quantum yield q as the number of quanta or the energy efficiency r as the amount of energy expended on a process in relation to the number of quanta or the amount of light energy absorbed by PSPs only; hence, the quantum yield in the stricter, narrower sense q – in relation to the number of quanta $N_{\mathrm{APSP}} \approx N_{\mathrm{APSP1}} + N_{\mathrm{APSP2}}$ or the energy efficiency in the very much narrower sense r – in relation to the amount of energy $E_{\mathrm{APSP}} \approx E_{\mathrm{APSP1}} + E_{\mathrm{APSP2}}$, neglecting absorption by PPPs:

- Energy efficiency of chlorophyll a fluorescence

$$r_{\mathrm{fl}} = E_{\mathrm{fl}}/E_{\mathrm{APSP}}. \tag{7}$$

- Quantum yield of chlorophyll a fluorescence

$$q_{\mathrm{fl}} = N_{\mathrm{fl}}/N_{\mathrm{APSP}}. \tag{8}$$

- Energy efficiency of photosynthesis

$$r_{\mathrm{ph}} = E_{\mathrm{ph}}/E_{\mathrm{APSP}}. \tag{9}$$

- Quantum yield of photosynthesis

$$q_{\mathrm{ph}} = N_{\mathrm{ph}}/N_{\mathrm{APSP}}. \tag{10}$$

- Energy efficiency of the radiationless conversion of the PSP molecule excitation energy into heat

$$r_H = E_{H2}/E_{\mathrm{APSP}}, \tag{11}$$

where $E_{H2} = E_{\mathrm{APSP}} - (E_{\mathrm{fl}} + E_{\mathrm{ph}})$.

- Quantum yield of the radiationless conversion of the PSP molecule excitation energy into heat

$$q_H = N_{H2}/N_{\mathrm{APSP}}, \tag{12}$$

where $N_{H2} = N_{\mathrm{APSP}} - (N_{\mathrm{fl}} + N_{\mathrm{ph}})$.

The upshot is that the distribution of the excitation energy of phytoplankton pigment molecules among the various processes can be analysed in four ways with reference to the four types of yield/efficiency outlined above, i.e. Φ, q, R, r. The sums of the quantum yields or energy efficiencies of these complementary processes expending the excitation energy of pigment molecules is equal to 1:

$$\Phi_{\text{fl}} + \Phi_{\text{ph}} + \Phi_H = 1, \tag{13}$$

$$q_{\text{fl}} + q_{\text{ph}} + q_H = 1, \tag{14}$$

$$R_{\text{fl}} + R_{\text{ph}} + R_H = 1, \tag{15}$$

$$r_{\text{fl}} + r_{\text{ph}} + r_H = 1. \tag{16}$$

The quantum yields/energy efficiencies of these three deactivation processes take values that vary widely in different seas and at different times. They are especially strongly affected by the irradiance conditions in the sea, the trophic type of sea water and to a lesser extent the water temperature. This is borne out by the results of empirical studies of these processes by numerous authors in various sea regions, and also by their statistical and modelled generalizations. Many of these studies, however, refer to just one of these deactivation processes – photosynthesis (Koblentz-Mischke et al. 1985, Morel 1991, Antoine et al. 1996, Antoine & Morel 1996, Ficek 2001) or to the Sun-Induced Chlorophyll *a* Fluorescence (SICF) (e.g. Babin et al. 1995, Maritorena et al. 2000, Morrison 2003, Huot et al. 2005, Huot et al. 2007). In contrast, only a few papers give the results of experimental studies or statistical and model generalizations of the yields/efficiencies of all three processes. For example, the study by Westberry & Siegel (2003), carried out in the north-western Sargasso Sea in 1992–1997, presents the results of simultaneous comprehensive empirical investigations (including the use of remote sensing methods) of all three processes. It provides valuable data on the long-term regularities governing changes in time and marine space, absolute values of the quantum yields of the three processes, and information on the interrelations among them in the context of the variability of environmental conditions in the Sargasso Sea. On the other hand, Ostrowska (2011, 2012a,b) successively developed a preliminary but unique, semi-empirical, mathematical model describing the dependences of the quantum yields of the three processes on the three principal factors governing phytoplankton growth in the sea, namely, the surface chlorophyll *a* concentration $C_a(0)$ (the trophic index of the sea water), the light conditions and the temperature at different depths in the water. Universally applicable to the different environmental conditions obtaining in the sea, this model is a synthesis of earlier models of the photosynthesis and fluorescence of marine phytoplankton (Woźniak et al. 1992, 2002, 2003, 2007, Ostrowska 2012a,b). We will be using these models in the present study to calculate the yields and efficiencies of the expenditure of pigment molecule excitation energy and its distribution among the three processes in various typical conditions prevailing in seas and oceans.

As we have already stated, the quantum yields and energy efficiencies of all three processes are strongly dependent on environmental factors. The models that we have developed here enable these yields/efficiencies to be determined to a good approximation on the basis of the three principal parameters governing the functioning of marine plant communities, that is, the trophic index of waters, measured by the surface concentration of chlorophyll a – $C_a(0)$, the underwater irradiance $PAR(z)$ and the temperature $temp(z)$ at various depths z in a basin.

The objective of this work is to analyse and define the variability in the yields/efficiencies of the processes deactivating excited phytoplankton pigment molecules under the various conditions prevailing in the World Ocean, that is, in different climatic zones, seasons, sea waters and at various depths in them. From such an analysis we can compare these yields/efficiencies and hence the full budgets of the phytoplankton pigment excitation energy expended on these three processes, which are complementary as regards the utilization of this energy. The methods and range of investigations undertaken in order to achieve this objective and the results obtained are given below. We analyse the various yields and efficiencies defined by equations (1)–(16), the values of which vary widely, in accordance with the nature of the processes that they describe.

2. The mathematical apparatus of the models and the range of calculations

2.1. The mathematical formulas used in the calculations

In the calculations we used a set of model formulas, listed in Table 1, covering the quantum yields (lines 1, 3, 5, 7, 8–12) and the energy efficiencies of the three processes (lines 2, 4, 6 8–12).

The quantum yields of chlorophyll a fluorescence (Φ_{fl} and q_{fl}), defined in the Introduction by eqs. (2) and (8), being the ratios of the number of quanta absorbed to the number of quanta emitted during fluorescence, are not equivalent to the corresponding ratios of the amounts of absorbed and emitted energy carried by these quanta; in other words, they are not equivalent to the energy efficiencies of fluorescence (R_{fl} and r_{fl}) as defined by eqs. (1) and (7). This due to the difference in the spectra of the absorbed and emitted light, i.e. the difference between the energy of the quanta absorbed by various pigments and the energy of the quanta emitted during chlorophyll a fluorescence. The differences between the quantum yields and the energy efficiencies vary in waters of different trophic types, and they also vary with depth in the sea. The energies of single quanta emitted by chlorophyll a during fluorescence are of course the same in all seas, and

Table 1. The mathematical apparatus of the models describing the dependence on environmental factors of the quantum yields and energy efficiencies of the deactivation of excited states in phytoplankton pigment molecules (photosynthesis, fluorescence and heat production) (*continued on next page*)

No.	Description	Basic equations	Remarks	Source
1	2	3	4	5
1	Quantum yield of chlorophyll *a* fluorescence	$\Phi_{\mathrm{fl}} = \Phi_{\mathrm{fl},0} + \Phi_{\mathrm{fl},v,\mathrm{MAX}}\, f_{\mathrm{fl},a}\, f_{\mathrm{fl},\Delta} \times$ $\times f_{\mathrm{fl},c(C_a(0))}\, f_{\mathrm{fl},c(PAR_{\mathrm{inh}})}\, f_{\mathrm{fl},E,t}$, $q_{\mathrm{fl}} = \Phi_{\mathrm{fl}/f_a} = (\Phi_{\mathrm{fl},0} + \Phi_{\mathrm{fl},v})/f_a =$ $= \Phi_{\mathrm{fl},0}/f_a + \Phi_{\mathrm{fl},v,\mathrm{MAX}}\, f_{\mathrm{fl},\Delta} \times$ $\times f_{\mathrm{fl},c(C_a(0))}\, f_{\mathrm{fl},c(PAR_{\mathrm{inh}})}\, f_{\mathrm{fl},E,t}$		Ostrowska (2012a)
2	Energy efficiency of chlorophyll *a* fluorescence	$R_{\mathrm{fl}} = \Phi_{\mathrm{fl}}(hc_0/\lambda_{\mathrm{fl}})X$, $r_{\mathrm{fl}} = q_{\mathrm{fl}}(hc_0/\lambda_{\mathrm{fl}})X$		given in this paper
3	Quantum yield of photosynthesis	$\Phi_{\mathrm{ph}} = \Phi_{\mathrm{ph},\mathrm{MAX}}\, f_a f_\Delta\, f_{c(C_a(0))} \times$ $\times f_{c(PAR_{\mathrm{inh}})}\, f_{E,t}$, $q_{\mathrm{ph}} = \Phi_{\mathrm{ph}}/f_a = \Phi_{\mathrm{ph},\mathrm{MAX}} \times$ $\times f_\Delta\, f_{c(C_a(0))}\, f_{c(PAR_{\mathrm{inh}})}\, f_{E,t}$		Woźniak et al. (2002, 2007)
4	Energy efficiency of photosynthesis	$R_{\mathrm{ph}} = \Phi_{\mathrm{ph}}\, \Phi_{\mathrm{MAX}}(C/NA)\, kepX$, $r_{\mathrm{ph}} = q_{\mathrm{ph}}\, \Phi_{\mathrm{MAX}}(C/NA)\, kep\, X$		given in this paper
5	Quantum yield of radiationless nonphotochemical deactivation	$\Phi_H(z) = 1 - (\Phi_{\mathrm{fl}}(z) + \Phi_{\mathrm{ph}}(z))$, $q_H(z) = 1 - (q_{\mathrm{fl}}(z) + q_{\mathrm{ph}}(z)) =$ $= 1 - (\Phi_{\mathrm{fl}} + \Phi_{\mathrm{ph}})/f_a$		Ostrowska (2012b)
6	Energy efficiency of radiationless nonphotochemical deactivation	$R_H = 1 - (R_{\mathrm{ph}} + R_{\mathrm{fl}})$, $r_H = 1 - (r_{\mathrm{ph}} + r_{\mathrm{fl}})$		given in this paper
7	Component $\Phi_{\mathrm{fl},0}$	$\Phi_{\mathrm{fl},0} = 0.00712 C_a(0)^{-0.402}$		Ostrowska (2012a)

Table 1. (*continued*)

1	2	3	4	5
8	The non-photosynthetic pigment absorption effect factor	$f_a = \dfrac{\tilde{a}^*_{\mathrm{pl,\,PSP}}}{\tilde{a}^*_{\mathrm{pl}}}$, where $\tilde{a}^*_{\mathrm{pl}} = f(C_a(0),\,\tau,\,PAR(0))$, $\tilde{a}^*_{\mathrm{pl,\,PSP}} = f(C_a(0),\,\tau)$ is definied by the algotrithm given in the Appendix in Woźniak et al. (2002),	$f_{\mathrm{fl},\,a} = f_a$	Woźniak et al. (2002), Ostrowska (2012a)
9	The factor describing the reduction in the portion of functional PS2 RC as a result of photoinhibition	$f_{c(PAR_{\mathrm{inh}})} = \exp\left(\dfrac{-4860746 PAR^2}{2.23^{temp/10}}\right)$, where $PAR = PAR(0)e^{-\tau}$	$f_{\mathrm{fl},\,c(PAR_{\mathrm{inh}})} =$ $= f_{c(PAR_{\mathrm{inh}})}$	Woźniak et al. (2007), Ostrowska (2012a)
10	The inefficiency factor in energy transfer and charge recombination	$f_\Delta \approx 0.408 \pm 0.105$	$f_{\mathrm{fl},\,\Delta} = f_\Delta$	Woźniak et al. (2007), Ostrowska (2012a)
11	The factor describing the effect of irradiance and temperature	$f_{E,\,t} = \left[1 - \exp\left(\dfrac{-PUR^*_{\mathrm{PSP}}}{5.23710^{-7} \times 2.03^{temp/10}}\right)\right] \times$ $\times \dfrac{5.237 \times 10^{-7} \times 2.03^{temp/10}}{PUR^*_{\mathrm{PSP}}}$, where $PUR^*_{\mathrm{PSP}} = PAR\,\tilde{a}^*_{\mathrm{pl,\,PSP}}$	$f_{\mathrm{fl},\,E,\,t} =$ $= 1 - f_{E,\,t}$	Woźniak et al. (2007), Ostrowska (2012a)
12	The factor describing the relation between the number of functioning PS2 RC and the trophicity of the water body	$f_{c(C_a(0))} = \dfrac{C_a(0)^{0.66}}{0.44 + C_a(0)^{0.66}}$	$f_{\mathrm{fl},\,c(C_a(0))} =$ $= 1 - f_{c(C_a(0))}$	Woźniak et al. (1992), Ostrowska (2012a)

where $h \approx 6.62 \times 10^{-34}$ J s (Planck's constant), $c_o = 299\,792\,458$ m s^{-1} (velocity of light in a vacuum), $\lambda_{\mathrm{fl}} = 683$ nm (wavelength of chlorophyll *a* fluorescence), $kep = 40000$ J g^{-1} (energy equivalent of carbon), X [10^{18} quanta J^{-1}] (quantum equivalent of energy), $C = 12$ g mol^{-1} (molar mass of carbon), $NA = 6.02 \times 10^{23}$ [mol^{-1}] (Avogadro number), $\Phi_{\mathrm{MAX}} = 0.125$ [atomC quantum^{-1}] (maximum yield of photosynthesis), $C_a(0)$ [mg m^{-3}] – total chlorophyll *a* concentration in the surface water layer, $\tilde{a}^*_{\mathrm{pl}}$, $\tilde{a}^*_{\mathrm{pl,\,PSP}}$ [m^2(mg tot. chl *a*)$^{-1}$] – mean mass-specific coefficient of light absorption of all pigments, and of only photosynthetic (PSP) pigments weighted by the irradiance spectrum, respectively, τ [dimensionless] – optical depth in the sea, PAR [μEin m^{-2} s^{-1}] – downward irradiance in the PAR spectral range, $temp$ [°C] – ambient water temperature, PUR^*_{PSP} [μEin (mg tot. chl *a*)$^{-1}$ s^{-1}] – mass-specific radiation flux absorbed by photosynthetic pigments.

are equal to $hc_o/\lambda_{\rm fl}$, where $h = 6.62517 \times 10^{-34}$ J s – Planck's constant, $c_o \approx 3 \times 10^8$ m s^{-1} – velocity of light in a vacuum, $\lambda_{\rm fl} \approx 685$ nm – wavelength of light quanta emitted by chlorophyll *a*. But the spectral compositions, i.e. the energies of the quanta absorbed by phytoplankton pigments under diverse conditions in seas, are very different, not only because of the differences in the spectral distribution of underwater irradiance, but also because of the different composition of pigments, which will vary as a result of the photoacclimation of phytoplankton to the light spectrum prevailing at any given point in the sea (Babin et al 1996, Majchrowski 2001, Woźniak & Dera 2007). The relationship between the number of quanta and the energy of the light absorbed by phytoplankton pigments is given by the so-called quantum equivalent of light energy X, which is equal to the ratio of the number of quanta absorbed to the sum of their energies. By taking this equivalent X into account, we can calculate the energy efficiencies of fluorescence $R_{\rm fl}$ and $r_{\rm fl}$ on the basis of the corresponding quantum yields of this process $\Phi_{\rm fl}$ and $q_{\rm fl}$, using the equations given in Table 1 (lines 1, 2). For these calculations, we take the value of X that we calculated for the light absorbed by all phytoplankton pigments[1] using the equations from the earlier comprehensive light-photosynthesis model (Woźniak et al. 2003). The vertical distributions of X in sea waters of different trophic types and at different depths in the upper water layers, of thicknesses from 1 to 2 times the depth of the euphotic zone, are given in Figure 2. From the characteristics of the variability of X it becomes clear that the energy efficiencies of chlorophyll *a* fluorescence ($R_{\rm fl}$ and $r_{\rm fl}$) are usually somewhat lower than the quantum yields of this process ($\Phi_{\rm fl}$ and $q_{\rm fl}$), especially in oligotrophic, mesotrophic and weakly eutrophic basins.

Again, the energy efficiencies of photosynthesis ($R_{\rm ph}$ and $r_{\rm ph}$) are usually some four times smaller than the corresponding quantum yields of the process ($\Phi_{\rm ph}$ and $q_{\rm ph}$). This is because a minimum of eight quanta from all the light quanta absorbed by PSP molecules (together with the chlorophyll *a* molecules at the photosynthetic reaction centres) are required to close off the cycle of endoenergetic chemical reactions in photosynthesis leading to the assimilation of one atom of carbon, even though not all of the energy of these eight quanta is utilized in these reactions (Govindjee 1975, Najafpour 2012). The energy equivalent of organic carbon *kep* contained in various organic substances may fluctuate within quite wide limits, depending on the type of substance involved. For substances photosynthesized by phytoplankton this

[1]The values of this equivalent X calculated for light absorbed only by the photosynthetic pigments of phytoplankton are very similiar $X_{\rm PSP} \approx X$ (the difference is scarcely 2–4%).

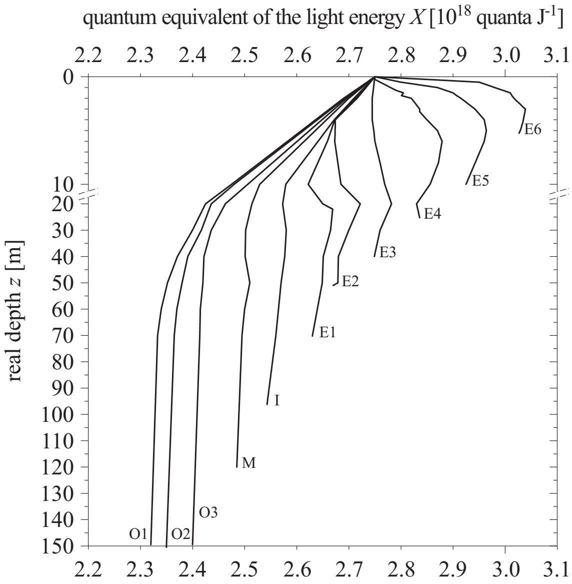

Figure 2. Vertical distributions of the quantum equivalent of the light energy absorbed by phytoplankton pigments X in sea waters of different trophic types (see Annex 2) and at different depths in the surface waters (calculated using the equations of the comprehensive light-photosynthesis model by Woźniak et al. 2003)

equivalent $kep \approx 40$ kJ g^{-1} (Koblentz Mischke et al. 1985). This calculation shows that for one atom of carbon to be assimilated, that is, for it to be bound in an organic form, the energy contained in two quanta of light from the visible spectrum is more than sufficient. The resulting relationships between the energy efficiencies (R_{ph} and r_{ph}) and quantum yields (Φ_{ph} and q_{ph}) of the photosynthesis of phytoplankton in the sea are given in Table 1, lines 2 and 4.

Likewise, the efficiencies of the conversion of pigment molecule excitation energy into heat (in the radiationless and nonphotochemical dissipation of this energy) R_H and r_H differ from the quantum yields of these processes Φ_H and q_H. This is because a certain amount of the energy of the quanta participating in photochemical reactions is dissipated: this energy is only partially consumed in the formation of the chemical bonds of organic compounds, while the remainder is dissipated in radiationless nonphotochemical processes. For this last reason, the energy efficiencies of these processes (R_H and r_H) are always greater than the corresponding quantum yields (Φ_H and q_H), that is, normally $R_H > \Phi_H$ and $r_H > q_H$. To calculate the energy efficiencies of heat production (R_H and r_H), we used the efficiencies, calculated earlier, of the other two accompanying processes, i.e. chlorophyll *a* fluorescence (R_{fl} and r_{fl}) and photosynthesis (R_{ph} and r_{ph}) and the budget equations (13)–(16) given in the Introduction.

2.2. The range of the model calculations and the input data

In order to characterize the different quantum yields and energy efficiencies of all three processes in which the excited states of phytoplankton pigment molecules are deactivated, the vertical profiles of these yields/efficiencies were modelled in sea waters of 11 trophic types (see Annex 2), in three climatic zones (tropical, temperate, polar) and in two seasons of the year (June – summer in the northern hemisphere and January – winter in the northern hemisphere). The model calculations of these yields/efficiencies were limited to oceanic Case 1 waters, according to the optical classification of Morel & Prieur (1977), which applies to more than 90% of the volume of the World Ocean. The three climatic zones of the ocean were represented by waters adjoining the relevant latitudes in the northern hemisphere: tropical (0–10°N), temperate (ca 40°N) and polar (ca 60°N). The input data for these model calculations made for different depths in the sea z (representing the fundamental variable) were:

- surface concentration of chlorophyll *a* $C_a(0)$, expressed in [mg chl$a$ m^{-3}],
- solar irradiance in the PAR spectral range (ca 400–700 nm) penetrating beneath the sea surface $PAR(0)$, expressed in [μEin m^{-2} s^{-1}],
- temperature in the surface layer of the sea *temp* expressed in [°C], which for simplicity was taken to be constant at all depths in this layer, in which practically all primary production takes place.

The surface layer temperatures *temp* and surface irradiances $PAR(0)$ were based on the geographical distributions and seasonal variations of these parameters, as given by Timofeyev (1983) and Gershanovich & Muromtsev (1982). The surface irradiances $PAR(0)$, expressed as the surface density of a stream of light quanta in [μEin m^{-2} s^{-1}], were calculated from the overall daily doses, given by those authors, of the energy of downward solar irradiance at the sea surface $< \eta_{\mathrm{day}} >_{\mathrm{month}}$ and the day length t_d [2] The specifications of these data are given in Table 2.

The values of the optical depth in the sea $\tau(z)$ [dimensionless], which were used directly to calculate the $PAR(z)$ irradiance and the yields/effi-

[2] $PAR(0)$ [μEin m^{-2} s^{-1}] $=< \eta_{\mathrm{day}} >_{\mathrm{month}}$ [MJ m^{-2} day^{-1}] 10^{12} A $\mathrm{T_S} X t_d^{-1}$[s] NA^{-1}, where A ≈ 0.5 is the typical proportion of PAR irradiance in the overall solar radiation, $X \approx 2.75 \times 10^{18}$ quanta J^{-1} is the typical value of the quantum equivalent of light energy at the sea surface, $\mathrm{T_S} \approx 0.95$ is the typical value of the PAR irradiance transmittance across the sea surface.

Table 2. Input data for the model calculations

Geographical zone	Season							
	Summer (June)				Winter (January)			
	$< \eta_{\mathrm{day}} >_{\mathrm{month}}$ [MJ m^{-2} day^{-1}]	t_d [h]	$PAR(0)$ [μEin m^{-2} s^{-1}]	*temp* [°C]	$< \eta_{\mathrm{day}} >_{\mathrm{month}}$ [MJ m^{-2} day^{-1}]	t_d [h]	$PAR(0)$ [μEin m^{-2} s^{-1}]	*temp* [°C]
tropical zone 0–10°N	19.6	12	985	27	18.6	12	934	25
temperate zone 40°N	21.4	14.8	872	20	8	9.5	508	10
polar zone 60°N	13.5	18.4	442	5	0.4	6.3	38.3	1

$< \eta_{\mathrm{day}} >_{\mathrm{month}}$ – monthly mean total daily doses of solar irradiance at the sea surface in different regions of the Word Ocean (after Timofeyev 1983).

t_d – approximate day length.

$PAR(0)$ – approximate value of PAR (in the 400–700 nm spectral range) just below the sea surface in different geographical regions (mean daily value in a given month).

temp – temperature of the water body in the upper sea layer (after Gershanovich & Muromtsev 1982).

ciencies of the three processes, were determined on the basis of the algorithm presented in Woźniak et al. (2003). They were worked out from a statistical model of the vertical distributions of chlorophyll a concentrations at particular depths in the sea $C_a(z)$ in stratified oceanic basins (Woźniak et al. 1992).

The input data listed in Table 2 and the definitions and models of quantum yields and energy efficiencies of the three processes for deactivating phytoplankton pigment excitation energies (photosynthesis, fluorescence and heat production) given in sections 1 and 2 (eqs. (1)–(16)) and the formulas in Table 1, were used to determine the yields/efficiencies for the three climatic zones and the two seasons. On this basis these excitation energy budgets were compared and contrasted in the context of the three complementary deactivation processes. The results of these calculations will now be analysed.

3. Results of the model calculations and discussion

We present the results of our model calculations for June (the northern hemisphere summer) and January (the northern hemisphere winter), divided into three climatic zones, in this section and in Annex 3. By way of example Figures 3–5 in subsection 3.1 show plots of the vertical distributions of quantum yields Φ (in the general, broader sense according to definitions (2), (4) and (6) respectively) of all three processes deactivating pigment molecule excitation energy in sea waters of different trophic types. Subsection 3.2, on the other hand, gives the ranges of seasonal variability of the components of the phytoplankton pigment excitation energy budget on the basis of the same quantum yields Φ averaged for the euphotic zone (Figure 6). The graphics and description cover the main features of the quantum yields, but the details of the calculations of selected characteristics of all four yields/efficiencies of the three processes are given in tabular form in Annex 3.

3.1. Vertical distributions of the quantum yields of fluorescence, photosynthesis and direct heat production by phytoplankton in oceans

The differentiation in the vertical distributions of the three elements of the phytoplankton pigment excitation energy budget is due, directly or indirectly, to the variability in irradiance conditions at different depths in the sea. This is illustrated in Figures 3, 4 and 5, which show depth profiles of the quantum yields Φ of all three processes in waters of different trophic types.

We can see from these plots that the quantum yield of the conversion of pigment molecule activation energy into heat Φ_H, (see plots b1, b2, b3 and

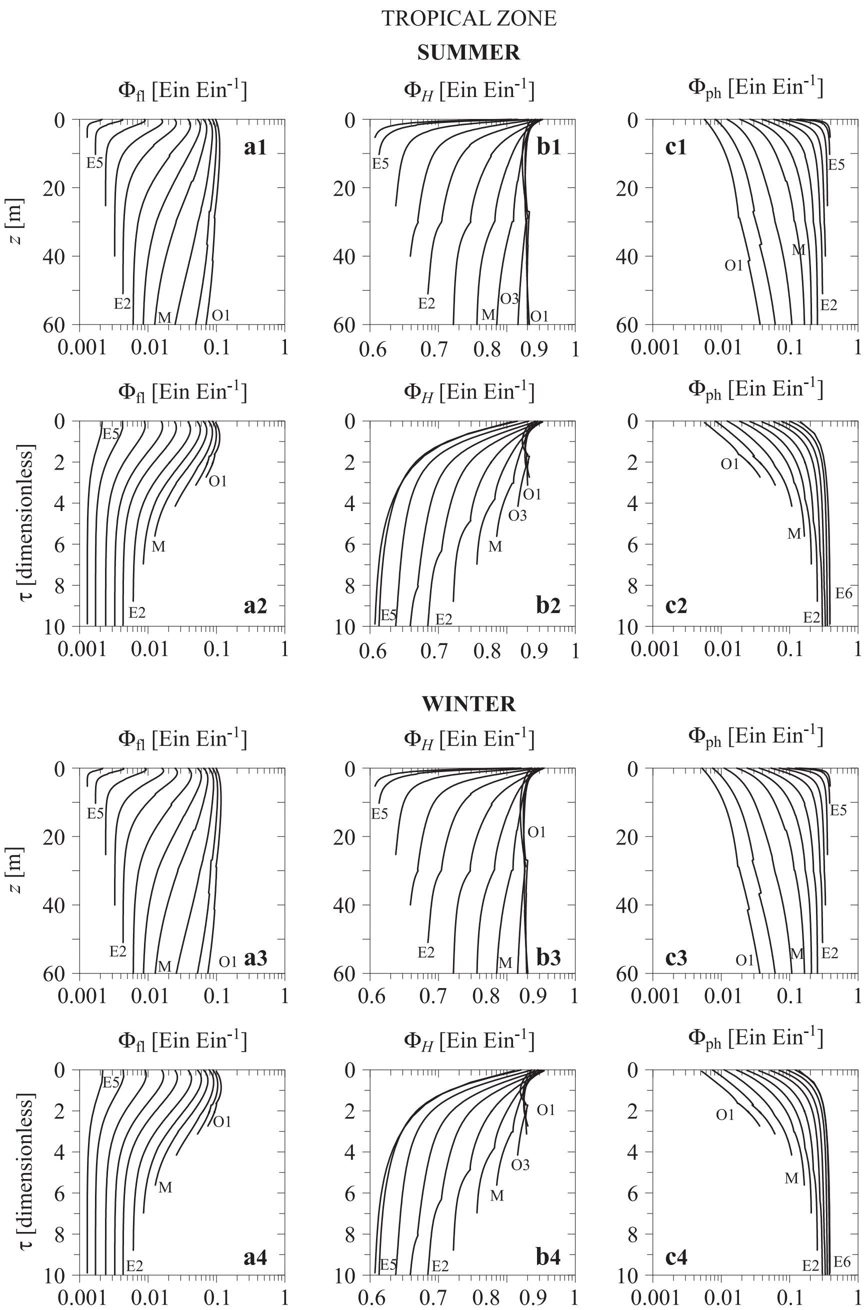

Figure 3. Modelled vertical profiles of quantum yields Φ (in the general, broader sense according to definitions (2), (4) and (6) respectively) of chlorophyll *a* fluorescence – Φ_{fl} (a), heat production – Φ_H (b) and photosynthesis – Φ_{ph} (c) of phytoplankton in tropical sea waters of different trophic type (explanation in the text)

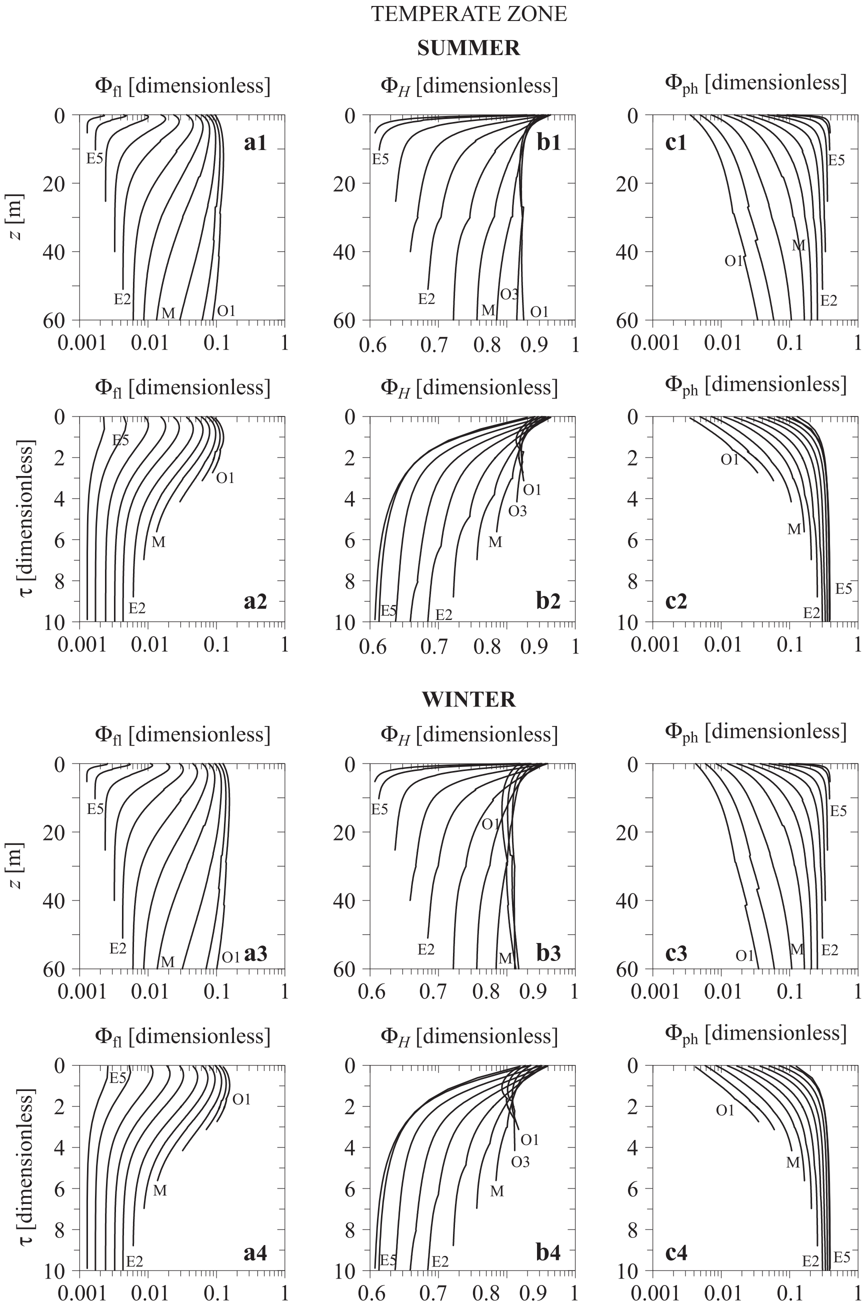

Figure 4. Modelled vertical profiles of quantum yields Φ (in the general, broader sense according to definitions (2), (4) and (6) respectively) of chlorophyll *a* fluorescence – Φ_{fl} (a), heat production – Φ_H (b) and photosynthesis – Φ_{ph} (c) of phytoplankton in temperate sea waters of different trophic type (explanation in the text)

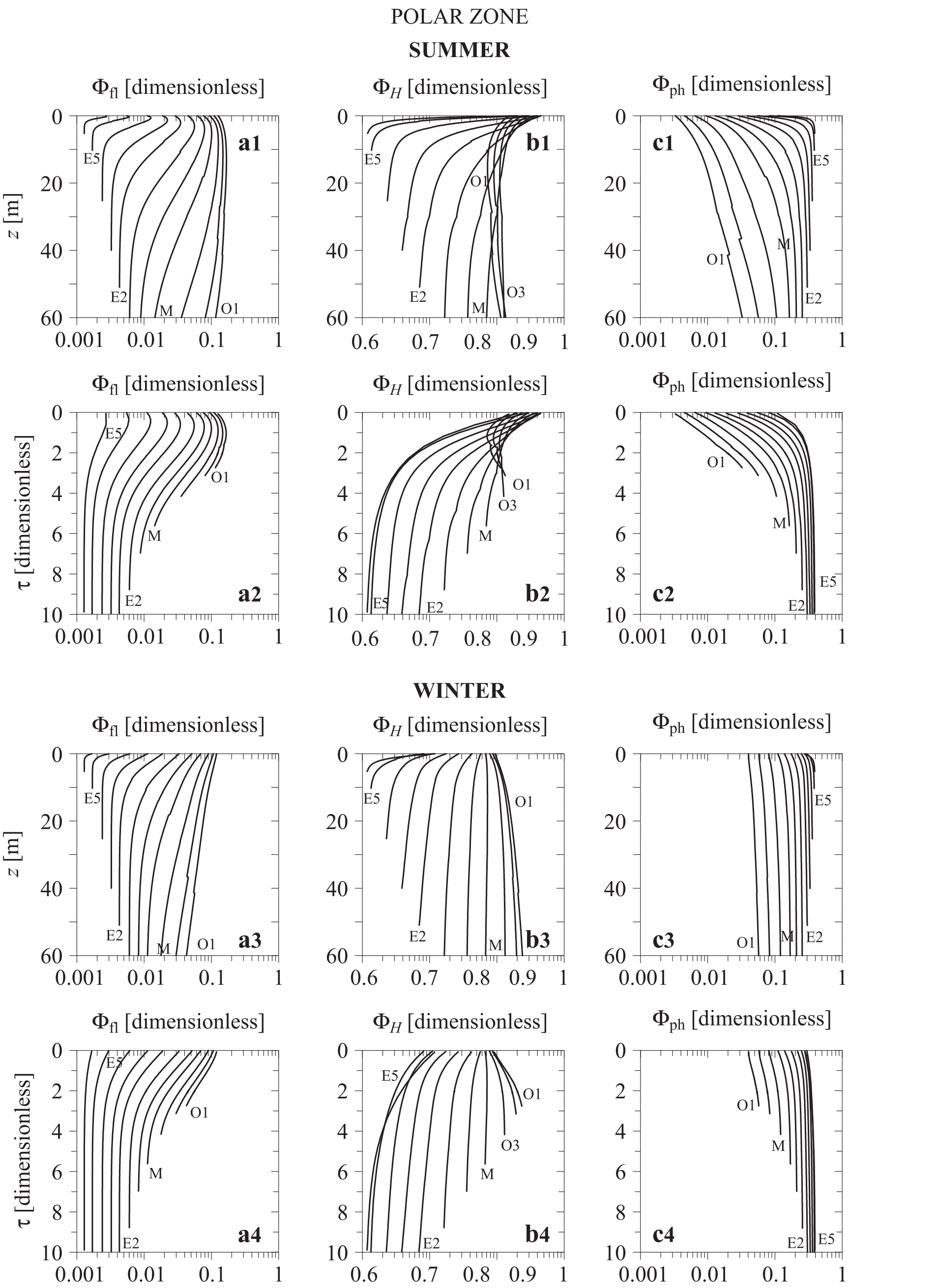

Figure 5. Modelled vertical profiles of quantum yields Φ (in the general, broader sense according to definitions (2), (4) and (6) respectively) of chlorophyll *a* fluorescence – Φ_{fl} (a), heat production – Φ_H (b) and photosynthesis – Φ_{ph} (c) of phytoplankton in polar sea waters of different trophic type (explanation in the text)

b4 in Figures 3, 4 and 5) is much or very much greater than the quantum yields of fluorescence Φ_{fl} (plots a1, a2, a3 and a4 on these figures) and photosynthesis Φ_{ph} (plots c1, c2, c3 and c4 on these figures) in every possible configuration of environmental factors in different geographical regions and seasons of the year. Values of Φ_H begin at ca 0.61 in the lower layers of eutrophic waters and increase with decreasing trophic index $C_a(0)$ and also with decreasing depth (i.e. with irradiance increasing towards the surface), especially in eutrophic waters though less so in mesotrophic ones, rising in some cases to 0.9 and even more. Most of the light energy absorbed by pigments is converted into heat. Quantum yields of heat production Φ_H are from ca 2 to 10 times greater than those of photosynthesis Φ_{ph} in the same waters and from as much as ca 20 to 150 times greater than those of fluorescence Φ_{fl}. Φ_{fl} and Φ_{ph} vary with depth in a slightly different way than Φ_H. Φ_{fl} usually takes the largest values near or at the surface of more eutrophic waters and, like Φ_H, decreases with increasing depth. On the other hand, Φ_{ph} has the smallest values at the surface and increases with depth, rising rapidly as the irradiance decreases with depth, but levelling out to a constant value in deeper waters; its values are always the largest in eutrophic waters, which are less transparent. Like Φ_{ph}, Φ_{fl} and Φ_H also level out to constant values at greater depths. But unlike Φ_{ph}, which reaches maximum values in waters of different trophic types, these constant values of Φ_{fl} and Φ_H are minima: this means that in water layers nearer the surface Φ_H and Φ_{fl} take somewhat higher or very much higher values. Again, unlike Φ_{ph}, the values of which rise with trophic index over the entire depth profile, Φ_H and Φ_{fl} generally behave in the opposite manner, that is to say, their values decrease with increasing trophic index.

The variabilities of Φ_{fl}, Φ_{ph} and Φ_H in every possible combination of environmental factors differ in scale. Φ_{fl} and Φ_{ph} vary within a wide range of values that may exceed one order of magnitude, but Φ_H does so within a narrow range, by less than a factor of two. The variability of all three yields is not significant in the tropical and temperate zones, but is the greatest and very considerable in polar waters. In most cases, this variability in the polar region forms an envelope, that is, it reaches both the minimum and the maximum values calculated for all three climatic zones. This regularity becomes clearer still for yields averaged over the entire euphotic zone of waters, as will be described in section 3.2.

3.2. Budgets for the deactivation of phytoplankton pigment excitation energy in waters of different trophic types

Apart from analysing the variations in the quantum yields and energy efficiences of these three deactivation processes at different depths in the sea, we also used the results of our model calculations to compare the energy budgets of these processes in waters of different trophic types in different geographical regions and seasons. The magnitudes characterizing the utilization of pigment molecule excitation energy in these processes are their energy efficiencies or quantum yields, averaged in the surface layer of waters penetrated by natural irradiance, weighted by the quantity of energy ($E_A(z)$ or $E_{\mathrm{APSP}}(z)$) or the number of quanta ($N_A(z)$ or $N_{\mathrm{APSP}}(z)$) absorbed by phytoplankton pigments at different depths in this layer. If we assume that the depth of water to which just 1% of PAR penetrates is z_e, that is roughly the depth of the euphotic zone, the average yields of these processes can be described by the following expressions:

$$< \Phi_i >_{z_e} = \left(\int_0^{z_e} N_A(z) dz \right)^{-1} \left(\int_0^{z_e} \Phi_i(z) N_A(z) dz \right), \tag{17}$$

$$< q_i >_{z_e} = \left(\int_0^{z_e} N_{\mathrm{APSP}}(z) dz \right)^{-1} \left(\int_0^{z_e} q_i(z) N_{\mathrm{APSP}}(z) dz \right), \tag{18}$$

$$< R_i >_{z_e} = \left(\int_0^{z_e} E_A(z) dz \right)^{-1} \left(\int_0^{z_e} R_i(z) E_A(z) dz \right), \tag{19}$$

$$< r_i >_{z_e} = \left(\int_0^{z_e} E_{\mathrm{APSP}}(z) dz \right)^{-1} \left(\int_0^{z_e} r_i(z) E_{\mathrm{APSP}}(z) dz \right), \tag{20}$$

where the subscript i denotes one of the three pigment molecule deactivation processes: $i = \mathrm{fl}$ – fluorescence, $i = \mathrm{ph}$ – photosynthesis, $i = H$ – radiationless nonphotochemical deactivation, i.e. heat production.

It is easy to grasp that these yields, averaged for the euphotic zone, supply information on the distribution of the energy or the number of quanta of radiation absorbed in the euphotic zone by phytoplankton pigments (all pigments or just PSPs) to drive the three processes. In other words, they represent the budgets for the amount of this energy (or the number of quanta) expended on the processes. The values of all these 12 quantum yields and energy efficiencies (i.e. linked with the four budget schemes according to equations (13) to (16)), and averaged according to equations (17) do (20), are given in Annex 3 in Tables A3.1 to A3.4 for waters of different trophic types (from oligotrophic type O1 with surface chlorophyll a concentration $C_a(0) = 0.035$ mg m^{-3} to the strongly eutrophic type E6 with surface chlorophyll a concentration $C_a(0) = 70$ mg m^{-3}) for summer and winter in three climatic zones. Figure 6 plots the calculated averaged in euphotic zone quantum yields of fluorescence $< \Phi_{\mathrm{fl}} >_{z_e}$, photosynthesis $< \Phi_{\mathrm{ph}} >_{z_e}$ and heat production $< \Phi_H >_{z_e}$. These yields are to be understood in the broader sense, that is, they refer to the total number of quanta absorbed by all phytoplankton pigments (both PSPs and PPPs).

The plots in Figure 6 (and also the numerical data in the relevant tables in Annex 3) show that there are differences in the natural values and ranges of variation of the three elements of the phytoplankton pigment excitation energy budget. As described in section 3.1, the yields of these processes at different depths in a basin, including the yields averaged over the euphotic zone, are the largest with respect to the radiationless conversion of activation energy into heat. The yields of photosynthesis are ca 5–15 times smaller, and the chlorophyll *a* fluorescence yields are the smallest: $< \Phi_H >_{z_e} > < \Phi_{\mathrm{ph}} >_{z_e} > < \Phi_{\mathrm{fl}} >_{z_e}$. In contrast, the regularities characterizing the ranges of variation of these terms in the overall budget are exactly the reverse. They are greatest with respect to the portion of energy consumed by the natural fluorescence of chlorophyll *a*, even though the energy efficiencies and quantum yields of this process are the least. For example, the quantum yield of fluorescence $< \Phi_{\mathrm{fl}} >_{z_e}$ (see Figures 6a and the data in Annex A3, Table A3.1) varies within a range covering almost two orders of magnitude (around 100 times), from ca 0.001 in supereutrophic polar waters in winter (E6) to ca 0.137 in ultra-oligotrophic polar waters (O1) in summer. The range of variation is slightly narrower in the case of the relative consumption of pigment excitation energy in photosynthesis. Here, the quantum yield, averaged for the euphotic zone $< \Phi_{\mathrm{ph}} >_{z_e}$ (see Figures 6b, and the data in Annex A3), varies with a range covering slightly

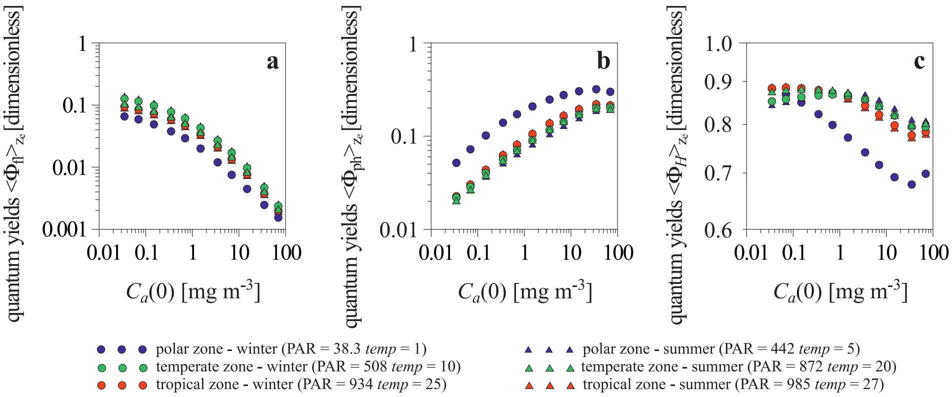

Figure 6. The characteristics of the quantum yields averaged for the euphotic zone of fluorescence $< \Phi_{\mathrm{fl}} >_{z_e}$ (a); of photosynthesis $< \Phi_{\mathrm{ph}} >_{z_e}$ (b); and of heat production $< \Phi_H >_{z_e}$ (c); by phytoplankton in sea waters of different trophic type, in different seasons and in different climatic zones

more than one order of magnitude (ca 13 times), from ca 0.022 in the ultra-oligotrophic waters (O1) of different climatic zones in both winter and summer to ca 0.319 in eutrophic polar waters (E5) in winter. Finally, the smallest range of variation, just ca 1.3 times, is characteristic of the radiationless nonphotochemical conversion of pigment excitation energy into heat. Quantum yields of heat production $< \Phi_H >_{z_e}$ (see Figure 6c, and the data in Annex A3) vary from ca 0.678, a value typical of eutrophic waters (E5), to ca 0.887 in oligotrophic tropical waters (O1) and (O2) in summer.

It is also worth having a look at the dependence of the separate aspects of the pigment excitation energy budget on (1) the surface chlorophyll *a* concentration $C_a(0)$, i.e. the trophic index of the water; (2) climatic zone and season. These relationships can be briefly summarized as follows:

- The trophic index is the factor most strongly differentiating the aspects of the overall energy budget recorded in nature. All the plots in Figure 6 show that this factor far outweighs any influence due to seasonal or climatic variation. This effect of the trophic index is of course different with respect to the various aspects of this budget. Trophic differences alter the amount of pigment excitation energy expended in the euphotic zone on chlorophyll *a* fluorescence by nearly two orders of magnitude, on photosynthesis by about one order and on heat production by a factor of ca 1.2. The nature of the dependence of these aspects of the budget on surface chlorophyll *a* concentration $C_a(0)$ is also different. The quantum yield of photosynthesis $< \Phi_{\mathrm{ph}} >_{z_e}$ (see Figures 6b) rises with increasing $C_a(0)$ across almost the whole range of variability. Only in supereutrophic basins E6 is there a slight drop in this quantum yield, which is undoubtedly due to the very much smaller thickness of well illuminated water in the euphotic zone in which photosynthesis takes place. The quantum yields of chlorophyll fluorescence $< \Phi_{\mathrm{fl}} >_{z_e}$ and heat production $< \Phi_H >_{z_e}$ display opposite tendencies, however: $< \Phi_{\mathrm{fl}} >_{z_e}$ decreases exponentially with the increase in $C_a(0)$ over the entire range of this trophic index (see Figure 6a), and likewise, the yield of heat production $< \Phi_H >_{z_e}$ decreases with rising $C_a(0)$ over a wide range of trophic types (see Figures 6c). The only slight divergences from this regularity occur in ultra-oligotrophic basins (O1 and O2) and in supereutrophic ones (E5 and E6), where $< \Phi_H >_{z_e}$ shows a slight tendency to increase with rising $C_a(0)$.
- Figure 6 shows that the irradiance conditions and temperatures resulting from seasonal and climatic changes do not seriously differentiate the various aspects of the overall budget of phytoplankton pigment excitation energy in different waters. If we ignore the extreme winter conditions in polar waters, these changes are no greater, and are

usually far less than 1.5 times with respect to the yields of fluorescence and photosynthesis and usually only a few per cent with respect to the yield of heat production.

4. Summary and final comments

Previously derived by the authors and modified for the purposes of the present work, the model descriptions of the three principal processes in which the excitation energy of marine phytoplankton pigments is deactivated, that is, the natural fluorescence of chlorophyll *a*, photosynthesis and heat production, were used to calculate the quantum yields and energy efficiencies of these processes in sea waters of different trophic types, in different seasons and climatic zones, and at different depths in the sea. The results of these computations were used to analyse the range of variability of these processes in the World Ocean and to compare their absolute quantum yields and energy efficiencies – see section 3.

The results of these analyses of the quantum yields and energy efficiencies of these processes at different depths in various types of sea water are illustrated by the vertical distributions of the quantum yields $\Phi(z)$ (Figures 3–5). They show that the main factor causing the differentiation in these yields is the underwater irradiance $PAR(z)$. The yields thus mainly depend (directly or indirectly) on the variability in the irradiance conditions obtaining at different depths in the sea. In consequence, the vertical profiles of the yields $\Phi(z)$ of these three processes are distinctly different for each one. This is described in detail in section 3.1.

With the results of the calculations presented in section 3.2 it was also possible to examine and compare the overall budget of phytoplankton pigment excitation energies in waters of different trophic types, in different climatic zones and seasons. For this we used the quantum yields and energy efficiencies of the processes deactivating these energies, averaged for the euphotic zone and weighted with the energy or number of quanta absorbed by phytoplankton pigments at particular depths (see equations (17) to (20)). These calculations indicate that the factor most strongly differentiating the components of this budget in seas is the trophic index of the water, assumed to be equivalent to the surface concentration of chlorophyll *a* $C_a(0)$. The effect of this factor on the variability of the components of this budget far outweighs the influence of other factors like season or climatic zone (see the plots in Figure 6). Owing to the natural differences in $C_a(0)$, the variability of the process yields averaged over the euphotic zone $< \Phi_i >_{z_e}$ is almost two orders of magnitude with respect to fluorescence $< \Phi_{\mathrm{fl}} >_{z_e}$, that is, to the relative utilization of phytoplankton pigment excitation energy for chlorophyll *a* fluorescence. The same natural differences in trophic

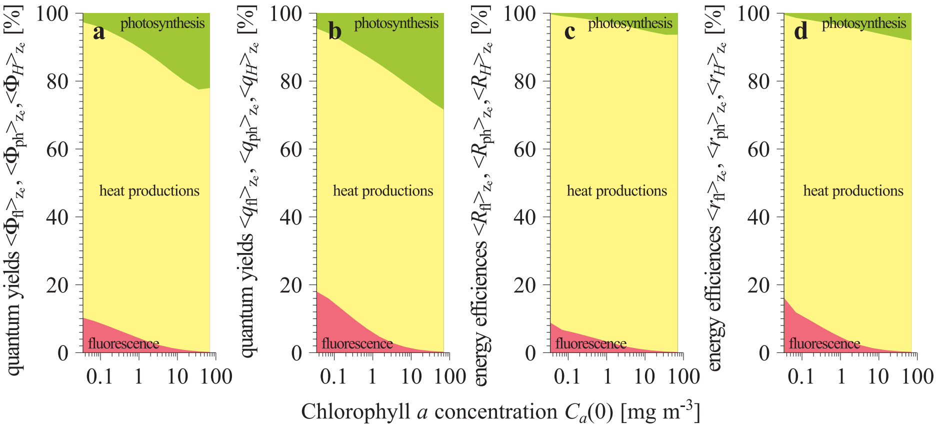

Figure 7. The complete budget of the number of absorbed quanta or the amount of excitation energy in phytoplankton pigments expended on the three deactivation processes, i.e. fluorescence ($<\Phi_{\rm fl}>_{z_e}$, $<q_{\rm fl}>_{z_e}$, $<R_{\rm fl}>_{z_e}$, $<r_{\rm fl}>_{z_e}$), heat production ($<\Phi_H>_{z_e}$, $<q_H>_{z_e}$, $<R_H>_{z_e}$, $<r_H>_{z_e}$) and photosynthesis ($<\Phi_{\rm ph}>_{z_e}$, $<q_{\rm ph}>_{z_e}$, $<R_{\rm ph}>_{z_e}$, $<r_{\rm ph}>_{z_e}$) as a function of the trophic type of water $C_a(0)$. The plots 7a, b, c d refer to the particular types of yield/efficiency defined by equations (1)–(12) and averaged as described in the text

index alter the average yield of photosynthesis $<\Phi_{\rm ph}>_{z_e}$ by one order of magnitude, but the yield of heat production $<\Phi_H>_{z_e}$ by only ca 1.2 times.

All the analyses carried out in this work, taking into account the various combinations of the main environmental factors acting on photosynthesis as well as the other two processes deactivating phytoplankton pigment excitation energy in sea waters, showed that the process leading to heat production is the most effective in all cases – see the plots in Figures 3, 4 and 5. For example, the quantum yield of heat production $\Phi_H(z)$ calculated for different depths in the sea z, is (for waters of the same trophic type) from ca 20 to 150 times greater than that of fluorescence $\Phi_{\rm fl}(z)$, and from 2 to 10 times larger than that of photosynthesis $\Phi_{\rm ph}(z)$. Evidence for the greater consumption of phytoplankton pigment excitation energy on heat production than on the other two processes is also provided by the calculated average and maxima/minima of the three processes in waters of different trophicity. These results are given in Annex 3 in Tables A3.5 and A3.6, and also on the plots in Figure 7.

Table A3.5 gives the ranges and average quantum yields of the fluorescence ($<\Phi_{\rm fl}>_{z_e}$, $<q_{\rm fl}>_{z_e}$), heat production ($<\Phi_H>_{z_e}$, $<q_H>_{z_e}$) and photosynthesis ($<\Phi_{\rm ph}>_{z_e}$, $<q_{\rm ph}>_{z_e}$) expressed as percentages of the number of quanta consumed by phytoplankton in the euphotic zone. Each of these average yields in waters of different trophic types, given in Table A3.5, is the arithmetic mean of the set of six average values weighted by the yield within the euphotic zone (calculated using equations (17) and (18) respectively), i.e. the values for two seasons in three climatic zones. The maximum and minimum values given in this table are respectively the largest and smallest of this set of six values. Analogously, the typical ranges and average energy efficiencies of fluorescence ($< R_{\rm fl} >_{z_e}$, $< r_{\rm fl} >_{z_e}$), heat production ($< R_H >_{z_e}$, $< r_H >_{z_e}$) and photosynthesis ($< R_{\rm ph} >_{z_e}$, $< r_{\rm ph} >_{z_e}$), expressed as percentages of the energy consumed by phytoplankton in the euphotic zone are given in Annex 3, Table A3.6. The plots in Figure 7 illustrate the complete budget of the number of absorbed quanta or the amount of excitation energy in phytoplankton pigment molecules expended on the three deactivation processes under scrutiny here. They represent the ranges of their values come across in sea waters of different trophic types and normalized to 100%, and refer to all four types of yield/efficiency, i.e. Φ, q, R, r defined by equations (1) to (12) and averaged over the euphotic zone according to equations (17) to (20), as described above (see plots 7a, b, c, d). These data show that heat production is much or very much greater than fluorescence or photosynthesis in waters of all trophic types and in every possible combination of environmental factors. For example, the average portion of heat production in the overall excitation energy budget, illustrated in Figure 7c, is always in excess of 90% and decreases only slightly with increasing $C_a(0)$. We demonstrate this by analysing the energy efficiencies $< R_{\rm fl} >_{z_e}$, $< R_H >_{z_e}$ and $< R_{\rm ph} >_{z_e}$, averaged as above, that is, with reference to the total amount of energy absorbed by phytoplankton pigments in the water column throughout the euphotic zone. The portions of fluorescence and photosynthesis in this budget are much lower. The average portion of fluorescence is ca 10% in oligotrophic waters of type O1 and falls with increasing trophic index, reaching values approaching zero ($<1\%$) in supereutrophic waters. On the other hand, the mean portion of photosynthesis in this budget is less than 1% in oligotrophic waters O1 and increases with increasing trophicity to a value of around 6% in supereutrophic waters.

In conclusion, we would like to draw attention to the fact that the characteristics of the energy budget (or number of quanta) of phytoplankton pigment molecules activated on absorbing solar radiation, for various typical conditions obtaining in the World Ocean, are based on a fairly sparse set of empirical data and to a large extent consist as yet of insufficiently tested theoretical assumptions and indirect analyses. These results should therefore be treated as preliminary ones, requiring further theoretical study and above all comprehensive simultaneous empirical investigations of all the three processes. At the same time, the traditional techniques and technologies of oceanographic research, based as they are on measurements and observations usually made on board a ship, can no longer satisfy these requirements. Research carried out in this way is costly and yet not very effective, because in practice the results refer to stations widely scattered in the sea water and in time. A solution to this problem and considerable progress in this field is offered by remote sensing (satellite) techniques. Apart from the tried and tested ship-board research methods, never, more effective and less expensive ones are appearing, which make use of and appropriately interpret the measurements and observations obtained from satellite-mounted apparatus. These methods are being developed at great intensity by our research team (see e.g. Woźniak et al. (2008, 2011a and b), Darecki et al. (2008)), in order to make fuller use of remote sensing to improve these model descriptions of energy expenditure and quantum fluorescence, photosynthesis and heat production by phytoplankton in sea waters of different trophic types.

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Annex 1

Symbols and abbreviations used in text

Symbol	Denotes	Units
1	2	3
a	Light absorption coefficient	m^{-1}
a_{pl}	Absorption coefficient of phytoplankton	m^{-1}
$\tilde{a}_{\mathrm{pl}}$	Mean light absorption coefficient of all phytoplankton pigments weighted by the irradiance spectrum	m^{-1}
$\tilde{a}^*_{\mathrm{pl}}$	Mean mass-specific light absorption coefficient of all pigments weighted by the irradiance spectrum	m^2(mg tot. chl a)$^{-1}$
$\tilde{a}^*_{\mathrm{pl,\,PSP}}$	Mean mass-specific light absorption coefficient of photosynthetic pigments weighted by the irradiance spectrum	m^2(mg tot. chl a)$^{-1}$
C_a	Concentration of total chlorophyll a (i.e. sum of chlorophylls a + pheo derived spectrophotometrically)	mg tot. chl a m^{-3}
c_o	Velocity of light in a vacuum (c_o = 299 792 458)	m s^{-1}
C	Molecular mass of carbon $C = 12$	g mol^{-1}
E1, E2, E3, E4, E5, E6	Eutrophic waters of various types (see Annex 2)	
E_{APPP}	Energy absorbed by photoprotecting pigments (PPP) leading to excitation of pigment molecules	J
E_{APSP}	Energy absorbed by photosynthetic pigments (PSP) (E_{APSP1} - by chlorophyll a, E_{APSP2} - by accessory photosynthetic pigments) leading to excitation of pigment molecules; $E_{\mathrm{APSP}} \approx E_{\mathrm{APSP1}} + E_{\mathrm{APSP2}}$	J
E_A	Total energy absorbed by phytoplankton pigments; $E_A \approx E_{\mathrm{APPP}} + E_{\mathrm{APSP}}$	J
E_{H1}	Excitation energy of PPP molecules converted into heat	J
E_{H2}	Part of the excitation energy of chlorophyll a converted directly into heat by radiationless nonphotochemical processes	J
E_H	Total energy converted directly into heat $E_H \approx E_{H1} + E_{H2}$	J

Symbols and abbreviations used in text (*continued*)

1	2	3
E_i	Internal transfer of PSP excitation energy leading to excitation of the pigments in chlorophyll *a* molecules	J
E_{fl}	Part of the excitation energy of chlorophyll *a* emitted in the form of its fluorescence in spectral band 685 nm	J
E_{ph}	Part of the excitation energy of chlorophyll *a* converted into chemical energy by the photosynthesis of organic matter	J
$f_a = f_{\mathrm{fl},\,a}$	Non-photosynthetic pigment absorption factor	dimensionless
$f_\Delta = f_{\mathrm{fl},\,\Delta}$	Inefficiency factor in energy transfer and charge recombination	dimensionless
$f_{c(C_a(0))}$, $f_{\mathrm{fl},\,c(C_a(0))} = 1 - f_{c(C_a(0))}$	Factor describing the effect of surface chlorophyll *a* concentration on the portion of functional PS2 RC for photosynthesis and fluorescence respectively	dimensionless
$f_{c(PAR_{\mathrm{inh}})} = f_{c(PAR_{\mathrm{inh}})}$	Factor describing the reduction in the portion of functional PS2 RC as a result of photoinhibition	dimensionless
$f_{E,\,t}$	Classic dependence of photosynthesis on light and temperature, also known as the light curve of photosynthetic efficiency at a given temperature	dimensionless
$f_{\mathrm{fl},\,E,\,t} = 1 - f_{E,\,t}$	Factor describing the effect of irradiance and temperature on phytoplankton fluorescence	dimensionless
F_0	Constant fluorescence	arbitrary units
F_v	Variable fluorescence	arbitrary units
h	Planck's constant ($h = 6.62 \times 10^{-34}$)	J s
I	Intermediate (between mesotrophic and eutrophic) type of water (see Annex 2)	
kep	Energy equivalent of carbon ($kep = 40\,000$)	J g^{-1}
M	Mesotrophic waters (see Annex 2)	
NA	Avogadro number ($NA = 6.02 \times 10^{23}$)	mol^{-1}

Symbols and abbreviations used in text (*continued*)

1	2	3
N_{APPP}	Number of quanta absorbed by photoprotecting pigments (PPP) leading to exitation of pigment molecules	number of pieces
N_{APSP}	Number of quanta absorbed by PSPs (N_{APSP1} – by chlorophyll *a*, N_{APSP2} – by accessory photosynthetic pigments) leading to excitation of pigment molecules; $N_{\mathrm{APSP}} \approx N_{\mathrm{APSP1}} + N_{\mathrm{APSP2}}$	number of pieces
N_A	Number of quanta absorbed by phytoplankton pigments $N_A \approx N_{\mathrm{APPP}} + N_{\mathrm{APSP}}$	number of pieces
N_H	Total number of quanta directly converted into heat $N_H \approx N_{H1} + N_{H2}$	number of pieces
N_{H1}	Number of quanta absorbed by PPP molecules converted directly into heat	number of pieces
N_{H2}	Number of quanta absorbed by chlorophyll *a* converted directly into heat by non-photochemical processes	number of pieces
N_i	Number of quanta absorbed by PSP pigments molecules transfered to the chlorophyll *a* molecules	number of pieces
N_{fl}	Number of quanta absorbed by chlorophyll *a* emitted in the form of its fluorescence in the spectral band 685 nm	number of pieces
N_{ph}	Number of quanta absorbed by chlorophyll *a* molecules converted into chemical energy by the photosynthesis of organic matter	number of pieces
O1, O2, O3	Oligotrophic waters of various types (see Annex 2)	
PS2 RC	Reaction Centre in the photosynthetic apparatus	
PAR	Photosynthetically Available Radiation	
PAR	Downward irradiance in the PAR spectral range (400–700 nm)	μEin m^{-2} s^{-1}
$PAR(0)$	Downward irradiance in the PAR spectral range (400–700 nm) just below the surface	μEin m^{-2} s^{-1}
PPP	Photopotecting pigments in phytoplankton	
PSP	Photosynthetic pigments in phytoplankton	
PUR^*_{PSP}	Number of quanta absorbed by PSPs in unit time referred to unit mass of chlorophyll *a*	μEin (mg tot. chl *a*)$^{-1}$ s^{-1}

Symbols and abbreviations used in text (*continued*)

1	2	3
q_{fl}	Quantum yield of fluorescence in the narrower sense (with respect to quanta absorbed only by PSPs)	Ein Ein^{-1} i.e. dimensionless
q_{ph}	Quantum yield of photosynthesis of organic matter in the narrower sense (with respect to only those quanta absorbed by PSPs)	Ein Ein^{-1} i.e. dimensionless
q_H	Quantum yield of the radiationless conversion of the excitation energy directly into heat in the narrower sense (with respect to only those quanta absorbed by PSPs)	Ein Ein^{-1} i.e. dimensionless
r_{fl}	Energy efficiency of fluorescence in the narrower sense (with respect to only those energy absorbed by PSPs)	J J^{-1} i.e. dimensionless
r_{ph}	Energy efficiency of photosynthesis of organic matter in the narrower sense (with respect to only that energy absorbed by PSPs)	J J^{-1} i.e. dimensionless
r_H	Energy efficiency of the radiationless conversion of excitation energy directly into heat in the narrower sense (with respect to only that energy absorbed by photosynthetic pigments)	J J^{-1} i.e. dimensionless
R_{fl}	Energy efficiency of fluorescence in the broader sense (with respect to the energy absorbed by all phytoplankton pigments)	J J^{-1} i.e. dimensionless
R_{ph}	Energy efficiency of photosynthesis of organic matter in the broader sense (with respect to the energy absorbed by all phytoplankton pigments)	J J^{-1} i.e. dimensionless
R_H	Energy efficiency of the radiationless conversion of excitation energy directly into heat in the broader sense (with respect to the energy absorbed by all phytoplankton pigments)	J J^{-1} i.e. dimensionless
SICF	Sun-Induced Chlorophyll Fluorescence	
t_d	Duration of daylight	h or s
$temp$	Ambient water temperature	$^{\circ}$C
X	Quantum equivalent of the light energy absorbed by phytoplankton pigments	quanta J^{-1}

Symbols and abbreviations used in text (*continued*)

1	2	3
z	Real depth in the sea	m
z_e	Depth of the euphotic zone	m
$< \eta_{\mathrm{day}} >_{\mathrm{month}}$	Monthly mean total daily dose of solar irradiance at the sea surface in various regions of the World Ocean	MJ m^{-2} day^{-1}
λ	Light wavelength	nm
λ_{fl}	Wavelength of chlorophyll *a* fluorescence ($\lambda_{\mathrm{fl}} = 683$)	nm
τ	Optical depth in the sea	dimensionless
Φ	Quantum yield of photosynthesis	atomC quanta^{-1} or molC Ein^{-1}
Φ_{fl}	Quantum yield of fluorescence in the broader sense (with respect to the quanta absorbed by all phytoplankton pigments)	Ein Ein^{-1} i.e. dimensionless
$\Phi_{\mathrm{fl},\,0}$	Quantum yield of fluorescence, associated with the constant fluorescence F_0	Ein Ein^{-1} i.e. dimensionless
$\Phi_{\mathrm{fl},\,v}$	Quantum yield of fluorescence, associated with the variable fluorescence F_v	Ein Ein^{-1} i.e. dimensionless
Φ_{MAX}	Theoretical maximum possible quantum yield of photosynthesis ($\Phi_{\mathrm{MAX}} = 0.125$)	atomC quanta^{-1}
$\Phi_{\mathrm{ph,\,MAX}}$	Theoretical maximum possible quantum yield of photosynthesis ($\Phi_{\mathrm{ph,\,MAX}} = 1$)	molC Ein^{-1}
Φ_{ph}	Quantum yield of photosynthesis of organic matter in the broader sense (with respect to the quanta absorbed by all phytoplankton pigments)	Ein Ein^{-1} i.e. dimensionless
Φ_H	Quantum yield of the radiationless conversion of excitation energy directly into heat in the broader sense (with respect to the quanta absorbed by all phytoplankton pigments)	Ein Ein^{-1} i.e. dimensionless
$\Phi_{\mathrm{fl},\,v,\,\mathrm{MAX}}$	Theoretical maximum possible quantum yield of fluorescence	Ein Ein^{-1} i.e. dimensionless

Annex 2. Classification of sea waters into trophic types

The conventional classification of sea waters (ecosystems) into trophic types according to Woźniak et al. (1992)

Trophic type	Symbol	Range of concentration C_a [mg m^{-3}]	Mean concentration C_a [mg m^{-3}]
oligotrophic	O-1	0.02–0.05	0.035
	O-2	0.05–0.10	0.075
	O-3	0.10–0.20	0.15
mesotrophic	M	0.2–0.5	0.35
intermediate	I	0.5–1.0	0.75
eutrophic	E-1	1–2	1.5
	E-2	2–5	3.5
	E-3	5–10	7.5
	E-4	10–20	15
	E-5	20–50	35
	E-6	50–100	75

Annex 3. Numerical data characterizing the yields/efficiencies of fluorescence, photosynthesis and heat production by phytoplankton in the World Ocean, calculated from the model shown in Table 1 on the basis of the input data described in section 2, averaged for the euphotic zone

Table A3.1. Mean quantum yields (in the broader sense, according to definitions (2), (4) and (6)) of phytoplankton chlorophyll *a* fluorescence $< \Phi_{\mathrm{fl}} >_{z_e}$, heat production, $< \Phi_H >_{z_e}$ and photosynthesis $< \Phi_{\mathrm{ph}} >_{z_e}$, determined from model computations for sea waters of different trophic types (O1–E6) in different climatic regions (polar, temperate and tropical) and seasons (January and June), averaged in waters of the euphotic zone according to formula (17)

Table A3.1a. Quantum yield of chlorophyll *a* fluorescence in the general, broader sense $< \Phi_{\mathrm{fl}} >_{z_e}$

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
polar (60 N)	winter (January)	6.57E-02	5.89E-02	4.90E-02	3.78E-02	2.92E-02	1.99E-02	1.20E-02	7.53E-03	4.46E-03	2.46E-03	1.54E-03
	summer (June)	1.37E-01	1.24E-01	1.05E-01	8.30E-02	6.47E-02	4.57E-02	2.85E-02	1.82E-02	1.04E-02	5.03E-03	2.51E-03
temperate (40 N)	winter (January)	1.26E-01	1.14E-01	9.76E-02	7.73E-02	6.06E-02	4.30E-02	2.68E-02	1.70E-02	9.69E-03	4.67E-03	2.36E-03
	summer (June)	1.05E-01	9.42E-02	8.05E-02	6.44E-02	5.11E-02	3.66E-02	2.30E-02	1.47E-02	8.36E-03	4.07E-03	2.12E-03
tropical (0–10 N)	winter (January)	9.43E-02	8.52E-02	7.31E-02	5.89E-02	4.70E-02	3.39E-02	2.13E-02	1.35E-02	7.67E-03	3.76E-03	2.00E-03
	summer (June)	9.03E-02	8.14E-02	7.00E-02	5.65E-02	4.53E-02	3.27E-02	2.05E-02	1.30E-02	7.41E-03	3.65E-03	1.96E-03

Table A3.1b. Quantum yield of heat production in the general, broader sense, $< \Phi_H >_{z_e}$

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
polar (60 N)	winter (January)	8.82E-01	8.69E-01	8.49E-01	8.23E-01	7.99E-01	7.71E-01	7.41E-01	7.16E-01	6.92E-01	6.78E-01	6.99E-01
	summer (June)	8.43E-01	8.50E-01	8.58E-01	8.66E-01	8.72E-01	8.73E-01	8.67E-01	8.54E-01	8.35E-01	8.10E-01	8.07E-01
temperate (40 N)	winter (January)	8.52E-01	8.57E-01	8.62E-01	8.66E-01	8.68E-01	8.66E-01	8.56E-01	8.41E-01	8.20E-01	7.95E-01	7.94E-01
	summer (June)	8.75E-01	8.79E-01	8.81E-01	8.81E-01	8.79E-01	8.72E-01	8.58E-01	8.41E-01	8.20E-01	7.98E-01	8.02E-01
tropical (0–10 N)	winter (January)	8.83E-01	8.85E-01	8.83E-01	8.79E-01	8.72E-01	8.61E-01	8.42E-01	8.21E-01	7.98E-01	7.76E-01	7.83E-01
	summer (June)	8.87E-01	8.88E-01	8.85E-01	8.79E-01	8.71E-01	8.58E-01	8.38E-01	8.16E-01	7.92E-01	7.71E-01	7.79E-01

Table A3.1c. Quantum yield of photosynthesis in the general, broader sense $< \Phi_{\mathrm{ph}} >_{z_e}$

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
polar (60 N)	winter (January)	5.18E-02	7.25E-02	1.02E-01	1.40E-01	1.72E-01	2.09E-01	2.47E-01	2.77E-01	3.04E-01	3.19E-01	3.00E-01
	Summer (June)	2.02E-02	2.60E-02	3.64E-02	5.07E-02	6.36E-02	8.09E-02	1.04E-01	1.28E-01	1.55E-01	1.85E-01	1.91E-01
temperate (40 N)	winter (January)	2.19E-02	2.86E-02	4.02E-02	5.64E-02	7.11E-02	9.07E-02	1.17E-01	1.42E-01	1.71E-01	2.01E-01	2.03E-01
	summer (June)	2.04E-02	2.68E-02	3.83E-02	5.47E-02	7.03E-02	9.12E-02	1.19E-01	1.44E-01	1.72E-01	1.98E-01	1.95E-01

Table A3.1c. Quantum yield of photosynthesis in the general, broader sense $< \Phi_{\mathrm{ph}} >_{z_e}$ (*continued*)

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
tropical (0–10 N)	winter (January)	2.27E-02	3.03E-02	4.35E-02	6.26E-02	8.10E-02	1.05E-01	1.37E-01	1.65E-01	1.94E-01	2.20E-01	2.15E-01
	summer (June)	2.31E-02	3.09E-02	4.46E-02	6.45E-02	8.37E-02	1.09E-01	1.42E-01	1.71E-01	2.00E-01	2.25E-01	2.19E-01

Table A3.2. Mean quantum yields (in the stricter, narrower sense, according to definitions (8), (10) and (12)) of phytoplankton chlorophyll *a* fluorescence $< q_{\mathrm{fl}} >_{z_e}$, heat production, $< q_H >_{z_e}$ and photosynthesis $< q_{\mathrm{ph}} >_{z_e}$, determined from model computations for sea waters of different trophic types (O1–E6) in different climatic regions (polar, temperate and tropical) and seasons (January and June), averaged in waters of the euphotic zone according to formula (18).

Table A3.2a. Quantum yield of fluorescence in the stricter, narrower sense, $< q_{\mathrm{fl}} >_{z_e}$

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
polar (60 N)	Winter (January)	8.69E-02	7.74E-02	6.36E-02	4.81E-02	3.63E-02	2.43E-02	1.42E-02	8.77E-03	5.10E-03	2.85E-03	1.98E-03
	summer (June)	2.21E-01	1.97E-01	1.61E-01	1.20E-01	8.86E-02	5.93E-02	3.51E-02	2.16E-02	1.21E-02	5.86E-03	3.23E-03
temperate (40 N)	winter (January)	2.09E-01	1.87E-01	1.53E-01	1.14E-01	8.42E-02	5.63E-02	3.31E-02	2.03E-02	1.12E-02	5.44E-03	3.04E-03
	summer (June)	2.00E-01	1.77E-01	1.43E-01	1.05E-01	7.67E-02	5.05E-02	2.93E-02	1.78E-02	9.76E-03	4.76E-03	2.74E-03
tropical (0–10 N)	winter (January)	1.84E-01	1.63E-01	1.32E-01	9.74E-02	7.15E-02	4.71E-02	2.72E-02	1.64E-02	8.98E-03	4.41E-03	2.59E-03
	summer (June)	1.80E-01	1.59E-01	1.29E-01	9.47E-02	6.95E-02	4.57E-02	2.64E-02	1.58E-02	8.68E-03	4.28E-03	2.54E-03

Table A3.2b. Quantum yield of heat production in the stricter, narrower sense, $< q_H >_{z_e}$

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
polar (60 N)	winter (January)	8.44E-01	8.27E-01	8.04E-01	7.74E-01	7.49E-01	7.21E-01	6.92E-01	6.69E-01	6.48E-01	6.28E-01	6.14E-01
	summer (June)	7.47E-01	7.61E-01	7.83E-01	8.07E-01	8.24E-01	8.36E-01	8.36E-01	8.27E-01	8.09E-01	7.78E-01	7.51E-01
temperate (40 N)	winter (January)	7.55E-01	7.66E-01	7.84E-01	8.03E-01	8.17E-01	8.25E-01	8.22E-01	8.10E-01	7.91E-01	7.61E-01	7.35E-01
	summer (June)	7.61E-01	7.73E-01	7.89E-01	8.06E-01	8.18E-01	8.24E-01	8.19E-01	8.07E-01	7.90E-01	7.64E-01	7.45E-01
tropical (0–10 N)	winter (January)	7.71E-01	7.78E-01	7.89E-01	7.99E-01	8.05E-01	8.06E-01	7.97E-01	7.83E-01	7.64E-01	7.38E-01	7.20E-01
	summer (June)	7.74E-01	7.80E-01	7.89E-01	7.97E-01	8.02E-01	8.01E-01	7.91E-01	7.76E-01	7.57E-01	7.32E-01	7.14E-01

Table A3.2c. Quantum yield of photosynthesis in the stricter, narrower sense, $< q_{\mathrm{ph}} >_{z_e}$

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
polar (60 N)	winter (January)	6.86E-02	9.53E-02	1.32E-01	1.78E-01	2.15E-01	2.54E-01	2.94E-01	3.22E-01	3.47E-01	3.70E-01	3.84E-01
	summer (June)	3.25E-02	4.13E-02	5.57E-02	7.33E-02	8.71E-02	1.05E-01	1.28E-01	1.52E-01	1.79E-01	2.16E-01	2.45E-01
temperate (40 N)	winter (January)	3.63E-02	4.67E-02	6.31E-02	8.30E-02	9.88E-02	1.19E-01	1.45E-01	1.69E-01	1.98E-01	2.34E-01	2.61E-01
	summer (June)	3.89E-02	5.03E-02	6.79E-02	8.91E-02	1.06E-01	1.26E-01	1.51E-01	1.75E-01	2.01E-01	2.32E-01	2.52E-01

Table A3.2c. Quantum yield of photosynthesis in the stricter, narrower sense, $< q_{\mathrm{ph}} >_{z_e}$ (*contimued*)

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
tropical (0–10 N)	winter (January)	4.43E-02	5.81E-02	7.87E-02	1.04E-01	1.23E-01	1.47E-01	1.75E-01	2.01E-01	2.27E-01	2.58E-01	2.77E-01
	summer (June)	4.59E-02	6.05E-02	8.20E-02	1.08E-01	1.29E-01	1.53E-01	1.82E-01	2.08E-01	2.35E-01	2.64E-01	2.83E-01

Table A.3.3. Mean energy efficiency (in the broader sense, according to definitions (1), (3) and (5)), of phytoplankton chlorophyll *a* fluorescence $< R_{\mathrm{fl}} >_{z_e}$, heat production,$< R_H >_{z_e}$ and photosynthesis $< R_{\mathrm{ph}} >_{z_e}$, determined from model computations for sea waters of different trophic types (O1–E6) in different climatic regions (polar, temperate and tropical) and seasons (January and June), averaged in waters of the euphotic zone according to formula (19)

Table A3.3a. Energy efficiency of fluorescence in the general, broader sense, $< R_{\mathrm{fl}} >_{z_e}$

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
polar (60 N)	winter (January)	9.55E-02	4.28E-02	3.64E-02	2.88E-02	2.26E-02	1.56E-02	9.43E-03	6.00E-03	3.59E-03	2.00E-03	1.27E-03
	summer (June)	1.01E-01	8.94E-02	7.74E-02	6.26E-02	4.98E-02	3.56E-02	2.24E-02	1.45E-02	8.41E-03	4.09E-03	2.06E-03
temperate (40 N)	winter (January)	1.01E-01	8.25E-02	7.18E-02	5.83E-02	4.67E-02	3.35E-02	2.10E-02	1.35E-02	7.80E-03	3.79E-03	1.94E-03
	summer (june)	7.59E-02	6.79E-02	5.92E-02	4.86E-02	3.93E-02	2.86E-02	1.81E-02	1.17E-02	6.74E-03	3.31E-03	1.74E-03
tropical (0–10 N)	winter (January)	7.88E-02	6.15E-02	5.39E-02	4.45E-02	3.63E-02	2.65E-02	1.67E-02	1.07E-02	6.18E-03	3.06E-03	1.65E-03
	summer (June)	7.76E-02	5.89E-02	5.16E-02	4.27E-02	3.49E-02	2.55E-02	1.61E-02	1.04E-02	5.97E-03	2.96E-03	1.61E-03

Table A3.3b. Energy efficiency of heat production in the general, broader sense, $< R_H >_{z_e}$

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
polar (60 N)	winter (January)	8.93E-01	9.39E-01	9.38E-01	9.35E-01	9.32E-01	9.29E-01	9.24E-01	9.18E-01	9.12E-01	9.08E-01	9.14E-01
	summer (June)	8.98E-01	9.04E-01	9.14E-01	9.25E-01	9.34E-01	9.43E-01	9.50E-01	9.50E-01	9.48E-01	9.43E-01	9.43E-01
temperate (40 N)	winter (January)	8.98E-01	9.11E-01	9.18E-01	9.27E-01	9.35E-01	9.42E-01	9.48E-01	9.47E-01	9.44E-01	9.39E-01	9.40E-01
	summer (June)	9.23E-01	9.26E-01	9.31E-01	9.38E-01	9.42E-01	9.47E-01	9.50E-01	9.49E-01	9.45E-01	9.41E-01	9.42E-01
tropical (0–10 N)	winter (January)	9.20E-01	9.31E-01	9.35E-01	9.40E-01	9.43E-01	9.46E-01	9.46E-01	9.44E-01	9.40E-01	9.35E-01	9.37E-01
	summer (June)	9.21E-01	9.34E-01	9.37E-01	9.41E-01	9.43E-01	9.45E-01	9.46E-01	9.43E-01	9.38E-01	9.33E-01	9.36E-01

Table A3.3c. Energy efficiency of photosynthesis in the general, broader sense, $< R_{\mathrm{ph}} >_{z_e}$

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
polar (60 N)	winter (January)	1.11E-02	1.77E-02	2.54E-02	3.59E-02	4.53E-02	5.57E-02	6.67E-02	7.58E-02	8.44E-02	8.96E-02	8.52E-02
	summer (June)	9.10E-04	6.26E-03	8.95E-03	1.28E-02	1.65E-02	2.14E-02	2.80E-02	3.50E-02	4.33E-02	5.25E-02	5.49E-02
temperate (40 N)	winter (January)	1.16E-03	6.89E-03	9.90E-03	1.43E-02	1.85E-02	2.40E-02	3.14E-02	3.90E-02	4.77E-02	5.68E-02	5.83E-02
	summer (June)	9.66E-04	6.46E-03	9.42E-03	1.39E-02	1.83E-02	2.42E-02	3.19E-02	3.96E-02	4.80E-02	5.60E-02	5.62E-02

Table A3.3c. Energy efficiency of photosynthesis in the general, broader sense, $< R_{\mathrm{ph}} >_{z_e}$ (*continued*)

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
tropical (0–10 N)	winter (January)	1.44E-03	7.31E-03	1.07E-02	1.59E-02	2.11E-02	2.80E-02	3.68E-02	4.53E-02	5.43E-02	6.21E-02	6.16E-02
	summer (June)	1.56E-03	7.48E-03	1.10E-02	1.64E-02	2.18E-02	2.90E-02	3.82E-02	4.69E-02	5.59E-02	6.36E-02	6.28E-02

Table A3.4. Mean values of energy efficiency (in the stricter, narrower sense, according to definitions (7), (9) and (11)) of phytoplankton chlorophyll *a* fluorescence $< r_{\mathrm{fl}} >_{z_e}$, heat production, $< r_H >_{z_e}$ and photosynthesis, $< r_{\mathrm{ph}} >_{z_e}$, determined from model computations for sea waters of different trophic types (O1–E6) in different climatic regions (polar, temperate and tropical) and seasons (January and June), averaged in waters of the euphotic zone according to formula (20)

Table A3.4a. Energy efficiency of fluorescence in the stricter, narrower sense, $< r_{\mathrm{fl}} >_{z_e}$

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
polar (60 N)	winter (January)	1.21E-01	5.60E-02	4.69E-02	3.63E-02	2.79E-02	1.89E-02	1.12E-02	6.98E-03	4.12E-03	2.33E-03	1.64E-03
	summer (June)	1.69E-01	1.44E-01	1.20E-01	9.08E-02	6.82E-02	4.61E-02	2.75E-02	1.72E-02	9.74E-03	4.79E-03	2.68E-03
temperate (40 N)	winter (January)	1.74E-01	1.38E-01	1.14E-01	8.64E-02	6.49E-02	4.38E-02	2.60E-02	1.61E-02	9.06E-03	4.44E-03	2.52E-03
	summer (June)	1.59E-01	1.32E-01	1.08E-01	8.00E-02	5.92E-02	3.94E-02	2.30E-02	1.42E-02	7.89E-03	3.89E-03	2.27E-03
tropical (0–10 N)	winter (January)	1.69E-01	1.23E-01	1.00E-01	7.45E-02	5.53E-02	3.67E-02	2.14E-02	1.31E-02	7.25E-03	3.60E-03	2.15E-03
	summer (June)	1.71E-01	1.20E-01	9.75E-02	7.24E-02	5.37E-02	3.56E-02	2.07E-02	1.26E-02	7.01E-03	3.50E-03	2.10E-03

Table A3.4b. Energy efficiency of heat production in the stricter, narrower sense, $< r_H >_{z_e}$

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
polar (60 N)	winter (January)	8.65E-01	9.21E-01	9.20E-01	9.18E-01	9.15E-01	9.13E-01	9.09E-01	9.05E-01	8.99E-01	8.94E-01	8.90E-01
	summer (June)	8.30E-01	8.46E-01	8.67E-01	8.91E-01	9.09E-01	9.26E-01	9.38E-01	9.41E-01	9.40E-01	9.35E-01	9.28E-01
temperate (40 N)	winter (January)	8.24E-01	8.52E-01	8.71E-01	8.93E-01	9.09E-01	9.25E-01	9.35E-01	9.37E-01	9.36E-01	9.30E-01	9.24E-01
	summer (June)	8.39E-01	8.57E-01	8.76E-01	8.98E-01	9.13E-01	9.27E-01	9.36E-01	9.38E-01	9.36E-01	9.31E-01	9.27E-01
tropical (0–10 N)	winter (January)	8.27E-01	8.64E-01	8.81E-01	8.99E-01	9.13E-01	9.24E-01	9.31E-01	9.32E-01	9.29E-01	9.24E-01	9.20E-01
	summer (June)	8.26E-01	8.66E-01	8.83E-01	9.00E-01	9.13E-01	9.24E-01	9.30E-01	9.30E-01	9.28E-01	9.23E-01	9.18E-01

A3.4c. Energy efficiency of photosynthesis in the stricter, narrower sense,$< r_{\mathrm{ph}} >_{z_e}$

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
polar (60 N)	winter (January)	1.41E-02	2.33E-02	3.31E-02	4.58E-02	5.66E-02	6.80E-02	7.94E-02	8.83E-02	9.65E-02	1.04E-01	1.09E-01
	summer (June)	1.52E-03	9.58E-03	1.34E-02	1.85E-02	2.27E-02	2.80E-02	3.47E-02	4.16E-02	4.98E-02	6.04E-02	6.89E-02

A3.4c. Energy efficiency of photosynthesis in the stricter, narrower sense, $< r_{\mathrm{ph}} >_{z_e}$ (*continued*)

Region	Season	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
temperate (40 N)	winter (January)	2.00E-03	1.08E-02	1.52E-02	2.09E-02	2.58E-02	3.17E-02	3.91E-02	4.65E-02	5.50E-02	6.54E-02	7.35E-02
	summer (June)	2.02E-03	1.15E-02	1.61E-02	2.23E-02	2.75E-02	3.35E-02	4.09E-02	4.80E-02	5.58E-02	6.48E-02	7.08E-02
tropical (0-10 N)	winter (January)	3.08E-03	1.34E-02	1.88E-02	2.61E-02	3.21E-02	3.91E-02	4.74E-02	5.51E-02	6.33E-02	7.21E-02	7.80E-02
	summer (June)	3.44E-03	1.40E-02	1.97E-02	2.72E-02	3.36E-02	4.08E-02	4.93E-02	5.71E-02	6.52E-02	7.39E-02	7.97E-02

Table A3.5. Typical mean values and ranges of variability of the quantum yields of fluorescence ($< \Phi_{\text{fl}} >_{z_e}$, $< q_{\text{fl}} >_{z_e}$), heat production ($< \Phi_H >_{z_e}$, $< q_H >_{z_e}$) and photosynthesis ($< \Phi_{\text{ph}} >_{z_e}$, $< q_{\text{ph}} >_{z_e}$), expressed as percentages of the number of quanta consumed in each process of all the quanta absorbed by phytoplankton pigments in the euphotic zones of sea waters of different trophic types (eqs. (17)–(18))

Table A3.5a. Quantum yields in the general, broader sense

Quantum yield of	Value [%]	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
fluorescence	maximum	13.72	12.42	10.54	8.30	6.47	4.57	2.85	1.82	1.04	0.50	0.25
$< \Phi_{\text{fl}} >_{z_e}$	**mean**	**10.30**	**9.31**	**7.93**	**6.30**	**4.96**	**3.53**	**2.20**	**1.40**	**0.80**	**0.39**	**0.21**
	minimum	6.57	5.89	4.90	3.78	2.92	1.99	1.20	0.75	0.45	0.25	0.15
heat production	maximum	88.67	88.76	88.55	88.09	87.86	87.34	86.72	85.40	83.47	80.95	80.67
$< \Phi_H >_{z_e}$	**mean**	**87.03**	**87.11**	**87.00**	**86.56**	**86.00**	**85.03**	**83.37**	**81.47**	**79.27**	**77.14**	**77.74**
	minimum	84.26	84.98	84.93	82.25	79.86	77.14	74.08	71.58	69.20	67.84	69.87
photosynthesis	maximum	5.18	7.25	10.17	13.96	17.22	20.86	24.72	27.67	30.36	31.92	29.98
$< \Phi_{\text{ph}} >_{z_e}$	**mean**	**2.67**	**3.59**	**5.08**	**7.14**	**9.03**	**11.43**	**14.43**	**17.13**	**19.93**	**22.46**	**22.05**
	minimum	2.02	2.60	3.64	5.07	6.36	8.09	10.43	12.78	15.49	18.54	19.08

A3.5b. Quantum yields in the stricter, narrower sense

Quantum yield of	Value [%]	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
fluorescence	maximum	22.05	19.72	16.12	11.99	8.86	5.93	3.51	2.16	1.21	0.59	0.32
$< q_{\text{fl}} >_{z_e}$	**mean**	**18.00**	**16.02**	**13.02**	**9.65**	**7.11**	**4.72**	**2.76**	**1.68**	**0.93**	**0.46**	**0.27**
	minimum	8.69	7.74	6.36	4.81	3.63	2.43	1.42	0.88	0.51	0.29	0.20
heat production	maximum	84.45	82.73	80.43	80.68	82.43	83.59	83.65	82.67	80.90	77.82	75.14
$< q_H >_{z_e}$	**mean**	**77.56**	**78.11**	**78.99**	**79.77**	**80.26**	**80.23**	**79.31**	**77.86**	**75.97**	**73.33**	**71.33**
	minimum	74.70	76.15	78.31	77.41	74.89	72.13	69.17	66.92	64.79	62.75	61.39
photosynthesis	maximum	6.86	9.53	13.21	17.78	21.48	25.43	29.40	32.20	34.70	36.96	38.41
$< q_{\text{ph}} >_{z_e}$	**mean**	**4.44**	**5.87**	**7.99**	**10.58**	**12.63**	**15.05**	**17.93**	**20.46**	**23.10**	**26.21**	**28.40**
	minimum	3.25	4.13	5.57	7.33	8.71	10.48	12.84	15.17	17.89	21.59	24.54

Table A3.6. Typical ranges and mean energy efficiencies of fluorescence ($< R_{\rm fl} >_{z_e}$, $< r_{\rm fl} >_{z_e}$), heat production ($< R_H >_{z_e}$, $< r_H >_{z_e}$) and photosynthesis ($< R_{\rm ph} >_{z_e}$, $< r_{\rm ph} >_{z_e}$), expressed as percentages of the energy consumed in each process of all the energy absorbed by phytoplankton pigments in the euphotic zones of sea waters of different trophic types (averaged according to equations (19 to 20)

Table A3.6a. Energy efficiencies in the general, broader sense

Quantum yield of	Value [%]	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
fluorescence	maximum	10.12	8.94	7.74	6.26	4.98	3.56	2.24	1.45	0.84	0.41	0.21
$< R_{\rm fl} >_{z_e}$	**mean**	**8.83**	**6.72**	**5.84**	**4.76**	**3.83**	**2.76**	**1.73**	**1.11**	**0.64**	**0.32**	**0.17**
	minimum	7.59	4.28	3.64	2.88	2.26	1.56	0.94	0.60	0.36	0.20	0.13
heat production	maximum	92.31	93.94	93.82	94.09	94.32	94.72	95.00	95.04	94.82	94.34	94.31
$< R_H >_{z_e}$	**mean**	**90.89**	**92.41**	**92.90**	**93.42**	**93.81**	**94.20**	**94.39**	**94.19**	**93.79**	**93.34**	**93.51**
	minimum	89.33	90.43	91.36	92.46	93.21	92.87	92.39	91.82	91.20	90.84	91.35
photosynthesis	maximum	1.11	1.77	2.54	3.59	4.53	5.57	6.67	7.58	8.44	8.96	8.52
$< R_{\rm ph} >_{z_e}$	**mean**	**0.29**	**0.87**	**1.26**	**1.82**	**2.36**	**3.04**	**3.88**	**4.69**	**5.56**	**6.34**	**6.31**
	minimum	0.09	0.63	0.90	1.28	1.65	2.14	2.80	3.50	4.33	5.25	5.49

Table A3.6b. Energy efficiencies in the stricter, narrower sense

Quantum yield of	Value [%]	Trophic types of sea waters as defined in Annex 2										
		O1	O2	O3	M	I	E1	E2	E3	E4	E5	E6
fluorescence	maximum	17.42	14.45	11.98	9.08	6.82	4.61	2.75	1.72	0.97	0.48	0.27
$< r_{\rm fl} >_{z_e}$	**mean**	**16.04**	**11.88**	**9.77**	**7.34**	**5.49**	**3.68**	**2.16**	**1.34**	**0.75**	**0.38**	**0.22**
	minimum	12.12	5.60	4.69	3.63	2.79	1.89	1.12	0.70	0.41	0.23	0.16
heat production	maximum	86.46	92.06	92.00	91.79	91.55	92.71	93.77	94.11	94.05	93.48	92.84
$< r_H >_{z_e}$	**mean**	**83.52**	**86.74**	**88.30**	**89.98**	**91.21**	**92.30**	**92.99**	**93.05**	**92.82**	**92.29**	**91.78**
	minimum	82.38	84.59	86.68	89.07	90.90	91.31	90.94	90.48	89.94	89.40	88.95
photosynthesis	maximum	1.41	2.33	3.31	4.58	5.66	6.80	7.94	8.83	9.65	10.36	10.88
$< r_{\rm ph} >_{z_e}$	**mean**	**0.44**	**1.38**	**1.94**	**2.68**	**3.31**	**4.02**	**4.85**	**5.61**	**6.43**	**7.34**	**8.00**
	minimum	0.15	0.96	1.34	1.85	2.27	2.80	3.47	4.16	4.98	6.04	6.89