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Comparison of Euphotic Layer Criteria in Lakes

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Abstract

The water layer where photosynthesis takes place (euphotic zone) was studied, and criteria for determining its thickness were compared. Published works give alternative definitions of the euphotic depth: 1) the depth at which radiation falls to 1% of the subsurface irradiance in the photosynthetically active radiation (PAR) region of the spectrum; 2) the depth of some small constant value of downwelling irradiance; 3) the depth of the photocompensation point. We compared values of the euphotic depth obtained by these criteria with each other and with the depth where primary production approaches zero. The data describing the vertical distribution of irradiance in the PAR region (90 profiles) and primary production (41 profiles) in 13 Estonian and Finnish lakes collected in 1995–97 were used. Additionally, criteria 1 and 2 were investigated by model calculations. The regression formulae describing the relationship between criteria for of the euphotic zone and the level of zero primary production were obtained. The respective correlation coefficients were different for each criteria and depended on the conditions of the data collection. The relationship between the 1%-level and constant irradiance level was strong when the incoming irradiance varies within narrow limits. The 1%-depth, widely used in practice, corresponded well to the level where primary production approached zero. By our results the 1%-depth and the depth of some constant irradiance describe the zone of positive gross primary production rather than the zone of positive net production.

Key words: Optical properties of lakes, light field in lakes, photosynthesis in water

1. Introduction

The concept of the euphotic zone is widely used in marine biology and marine optics, being generally applied to the water layer, where photosynthesis takes place; however, practical determination of this layer is rather complicated. Numerous publications treat the euphotic zone as the water layer, at the lower boundary of which the photosynthetically active radiation (PAR) falls to 1% of that just below the water surface (depth denoted by $z_{1\%}$). Often the extent to which this criterion corresponds to the actual layer of photosynthesis is not discussed. The irradiance varies remarkably within the water column during the day. The thickness of the layer with light conditions suitable for photosynthesis depends on the absolute values of surface irradiance and the diffuse attenuation coefficient of water (the optical criteria for euphotic layer), and the properties of phytoplankton (species composition, light adaptations, concentration of chlorophyll *a*), temperature, etc. (they constitute biological criteria). As shown below, there are alternative definitions of the euphotic zone by different authors.

According to *Kirk* (1996, p. 144): "Significant phytoplankton photosynthesis takes place only down to that depth, at which the downwelling photosynthetically active radiation (PAR) falls to one per cent of that just below the surface. That layer is known as euphotic zone." There is no reference to any absolute level of irradiance in this definition.

However, by *Chekhin* (1987), the ratio of the depth of actual photosynthesis to the 1% depth is between 2.5 and 0.4. According to *Chekhin* (1987), the lowest level of underwater irradiance at which one can expect photosynthesis, is approximately 2.08 W m^{-2} (about 10 μmol s^{-1} m^{-2}). Also *Adamenko et al.* (1991) referring to the published data and to numerous experimental results obtained for Russian lakes, claim that there exists a lower limit of PAR for photosynthesis: 2.3–9.7 μmol $s^{-1}m^{-2}$ at a temperature from 4 °C to 20 °C.

According to *Tilzer* (1987) and *Horne and Goldman* (1994), the lower boundary of the euphotic zone is at the compensation point, where photosynthetic oxygen liberation equals the respiratory oxygen consumption. The irradiance at which the compensation point occurs, varies between 0.18 and 350 μmol $s^{-1}m^{-2}$, being lowest for ice-algae and highest for corals (*Kirk,* 1996).

In his monograph *Dera* (1992, p. 279) describes these criteria in a general manner: "Marine biology often delimits a euphotic zone in the sea, i.e., the upper layer of waters irradiated with enough daylight to make photosynthesis possible. The lower boundary of this zone is determined by an average level of diurnal irradiance at a given depth such that the amount of oxygen produced during photosynthesis falls to a level comparable with the quantity consumed by the same cells during respiration. This compensation depth, somewhat fluid and not very precisely defined, is roughly that at which the surface irradiance of photosynthetically active radiation falls to 1%."

The idealised objective of the investigation could be to find a universal and easily measurable criterion for determining the authentic value of the euphotic depth (i.e. the lower boundary of the layer where photosynthesis takes place); however, this is an extremely difficult task, and the existence of one, universal criterion is doubtful. In practical investigations the problems of the accuracy of results arise, because: 1) irradiance values in the subsurface layer are fluctuating due to wave action; 2) the sensitivity of the measuring instruments have its limits, making often impossible to determine the very small values of irradiance; 3) the lower boundary of the layer where photosynthesis takes place can be determined rather approximately (by measurements of primary production).

Despite these limitations, the problem of regulation of photosynthesis by light is important in marine biology and worthy of investigation. To decide which characteristic is the most suitable for describing the photosynthetically active layer in the water bodies under different conditions, *in situ* investigations of the geographical, seasonal and diurnal variability of different euphotic depth criteria for highly variable water properties are necessary. The present work can be considered as one contribution to this field:

1. to show the dependence of the numerical values of "optical" euphotic depths (1% level and a constant value of PAR) on the methods of their determination;
2. to compare these two optical criteria in different lakes under variable light conditions;
3. to investigate the mutual relationships between the "optical" euphotic depth and the euphotic layer assessed from measurements of primary production.

2. *Methods and measurements*

2.1 *Investigated lakes*

We had the underwater light data for 13 Estonian and Finnish lakes from the years 1995–97. These lakes have different water properties. Transparency (measured by Secchi disk) varied from 0.15 to 6.5 m, and the concentrations of chlorophyll *a*, yellow substance and suspended matter ranged between 0.4–130 mg/m^3, 0.3–90 mg/l and 1.2–145 mg/l, respectively. Additional information about these lakes can be found in *Arst et al.* (1996, 1999). In the present paper only some of the most relevant parameters are given (Table 1). Altogether we analysed 90 series of optical measurements and 41 measurement series of primary production.

Table 1. Mean values of Secchi depth (z_{Secchi} m), chlorophyll *a* concentration (C_{Chl}, mg m^{-3}), diffuse attenuation coefficients for downwelling ($K_{d,\mathrm{PAR}}$, m^{-1}) and scalar irradiance ($K_{0,\mathrm{PAR}}$, m^{-1}), primary production integrated over the depth (PP_{int}, mg C m^{-2} h^{-1}) and maximum primary production ($PP_{\max}$, mg C m^{-3} h^{-1}) in Estonian (E) and Finnish (F) lakes in 1995–97.

LAKE	z_{Secchi}	C_{Chl}	$K_{0,\mathrm{PAR}}$	$K_{d,\mathrm{PAR}}$	$PP_{\max}$	PP_{int}
Äntu Sinijärv (E)	Bottom seen (7 m)	0.55	0.24	0.29	1.8	2.3
Koorküla Valgjärv (E)	3.6	5.65	0.53	0.56	7.6	29.5
Nohipalu Valgjärv (E)	5.4	15.6	0.66	0.67	3.5	26.3
Päijänne (F)	4.8	1.5	0.74	0.78	–	–
Kurtna Nõmmejärv (E)	3.6	2.05	0.76	0.79	5.6	10.9
Vesijärvi (F)	2.5	13.9	0.83	0.93	–	–
Verevi (E)	2.4	12.5	0.96	1.12	11.4	36.4
Lammi Pääjärvi (F)	2.2	7.2	1.5	1.75	–	–
Uljaste (E)	2.1	24.5	1.81	1.94	16.3	28.1
Valkeakotinen (F)	0.95	8.1	2.97	3.15	–	–
Tuusulanjärvi (F)	0.53	35.9	3.25	3.30	–	–
Võrtsjärv (E)	0.65	63.5	3.72	4.46	57.4	62.7
Nohipalu Mustjärv (E)	0.59	23.9	6.62	8.78	0.24	0.2

2.2 Biological measurements

For chlorophyll *a* (C_{Chl}) measurements, seston was collected on Whatman glass fibre filters (GF/C). Pigments were extracted with 90% acetone and analysed spectrophotometrically (*Recommendations…*, 1979).

The relative transparency, z_{Secchi} (m), was measured in all lakes with a standard white Secchi disk. Primary production (*PP*) in Estonian and Finnish lakes was measured by the $^{14}CO_2$ assimilation technique first introduced by *Steeman-Nielse*n (1952). Water from 5–6 horizons within a surface water layer down to $3{\times}z_{\mathrm{Secchi}}$ depth was poured into scintillation vials and incubated in the lake for 2 hours at the same depths where the water samples were taken. Non-photosynthetic carbon fixation was measured in the dark using two vials with water from the surface layer and from the deepest horizon. The final radioactivity analysis of water samples was performed with LSC RackBeta (Wallac, Finland). *A priori* information and experimental data allowed us to consider $^{14}CO_2$ fixation during 2–4 hours of exposure to light as an approximate measure of gross photosynthesis in productive waters (*Nielsen and Briesta*, 1984; *Kirk,* 1996).

To assess the depths where the amount of specific primary production (*PP**) approached zero ($z_{PP=0}$) 41 cases in 7 Estonian lakes were suitable. Data from an extremely clear Lake Äntu Sinijärv and a very dark Lake Nohipalu Mustjärv were excluded, because of large relative errors both in optical and production measurements.

The depth of the compensation point, z_{comp}, was calculated as the depth where gross primary production and respiration of phytoplankton became equal (*Horne and Goldman,* 1994). Respiration (R) was calculated from chlorophyll *a* concentrations following *Giorgio and Peters* (1993):

$$R[\,mgCm^{-3}h^{-1}\,] = 1.9C^{0.56}. \tag{1}$$

From all collected data, we selected for our analysis 29 measurement series obtained for Estonian lakes, leaving out some cases when the calculated respiration exceeded $PP_{\max}$ and it was impossible to find z_{comp}.

2.3 Radiation measurements and characteristics

Both scalar and downwelling irradiances (PAR region of the spectrum) in the lakes were measured using LI–COR sensors: LI–193 SA for the scalar irradiance and LI–192 SA for the downwelling irradiance (*Jewson et al.* 1984, *Bowling and Tyler* 1985).

Incident irradiance in the range of 400–700 nm was measured by the LI–192 SA just before submerging it into the water and after the underwater measurements and with an air pyranometer LI–200 SA (range 400–1100 nm) during the measurement.

The sensitivity of the LI–192 SA and LI–193 SA did not allow us to reach high accuracy for very small values of radiation. The relative error of irradiance is 5%, but it increases at values of irradiance less than 50 μmol s^{-1} m^{-2}, to 23% for an irradiance of 25 μmol s^{-1} m^{-2}. Changes in the underwater irradiance due to the variation of incident irradiance (cloud cover) were taken into account following the method of *Virta and Blanco-Sequeiros* (1995) using the air pyranometer (LI-200 SA) data.

The monochromatic irradiance decreases exponentially with depth (for simplicity the wavelength index is omitted in Eq. (2) and later):

$$E_{d,0}(z) = E_{d,0}(z=-0)\, e^{-K_{d,0}z}, \tag{2}$$

where $K_{d,0}$ is the diffuse attenuation coefficient averaged over depth. Eq. (2) was assumed to be approximately valid also for PAR. Then the diffuse attenuation coefficient averaged over PAR and depth have to be used in Eq. (2) ($K_{d,0,\mathrm{PAR}}$). To determine this mean value of the attenuation coefficient a semilog plot of PAR irradiance results vs. depth is applied and $K_{d,0,PAR}$, is found as the slope of the least-square regression line through these points. The R^2 value of the exponential fit of measured irradiance values vs. depth is typically more than 0.97 and standard error of estimated diffuse attenuation coefficient from broad band measurements is 0.1 m^{-1}, but from spectral data this error is remarkably smaller: 0.01 m^{-1}. However, by *Bowling and Tyler* (1985) this method can lead to considerable errors in very clear or strongly heterogeneous lakes.

The depth $z_{1\%}$ can be calculated from the mean value of $K_{d,0}$:

$$z_{1\%} = \frac{\ln 100}{K_{d,0}} \cong \frac{4.6}{K_{d,0}}. \tag{3}$$

We assumed the lowest level of irradiance for photosynthesis to be 4 μmol $s^{-1}m^{-2}$ (z_4) as it corresponds to the depth of the compensation point for coastal waters by *Platt and Jassby* (1976) and is within the range estimated by *Adamenko et al.* (1991). Note that the exact value of "constant irradiance" is not important for the present discussion, because our purpose is to investigate the behaviour of some depth at fixed irradiance.

The depth with constant irradiance E_{const}=4 μmol s^{-1} m^{-2} (z_4) can be calculated also by applying the exponential law:

$$z_4 = \frac{1}{K_{d,0}} \ln \frac{E_{d,0,PAR}(z=-0)}{E_{const}}, \tag{4}$$

where $E_{d,0}$(z=-0) is subsurface PAR. Two groups of initial data were used: (1) the values of $E_{d,0,\mathrm{PAR}}$(z=-0) and $K_{d,0,\mathrm{PAR}}$ from PAR measurements; (2) spectral values of K_d for some Estonian and Finnish lakes from paper by *Reinart and Herlevi* (1999) and modelled spectral incident PAR by *Bird and Riordan* (1986).

3. Results

3.1 Underwater irradiance and diffuse attenuation coefficient of PAR

Both scalar and downwelling vector irradiances show an approximately exponential decline throughout the water column. There is some dependence of the E_0/E_d ratio on water transparency: in the most turbid lakes (Võrtsjärv and Tuusulanjärvi) this ratio is 1.7–2.3, in clear lakes it varies from 1.3 to 1.6 and in the lakes with a high amount of dissolved organic matter (Nohipalu Mustjärv, Lammi Pääjärvi, Valkeakotinen) from 1.5–2.0. Such dependence may be caused by high absolute values of scattering and backscattering in turbid waters and high absorption values in brown lakes. These results are in good agreement with the data of *Højerslev* (1978) and *Kirk* (1981), by which the $E_{0,\mathrm{PAR}}/E_{d,\mathrm{PAR}}$ ratio is 1.2 in open ocean, varies mostly from 1.25 to 1.8 in inland waters and increases to 2.0–2.5 in very turbid lakes. According to *Jerome et al.* (1990), the scalar irradiance at a given depth may be even greater than twice the downwelling irradiance at that depth. Downward vector irradiance underestimates the amount of light available for photosynthesis (particularly in turbid waters). By our measurements this underestimate is in the range of 23–56%.

The mean values of $K_{d,\mathrm{PAR}}$ and $K_{0,\mathrm{PAR}}$ for PAR are shown in Table 1 (these values are averaged for each lake). The diffuse attenuation coefficient for downward plane irradiance is close to that for scalar irradiance. In most lakes the $K_{d,\mathrm{PAR}}/K_{0,\mathrm{PAR}}$ ratio is between 1.01 and 1.07 and in some cases it is up to 1.2–1.3. By Monte Carlo simulations *Kirk* (1996) found $K_{d,\mathrm{PAR}}/K_{0,\mathrm{PAR}}$ to be between 1.01 and 1.06 using a scattering phase function, that may differ from that in freshwater lakes rich in mineral particles. We obtained higher values namely for very clear Lake Äntu Sinijärv probably due to reflection from the bottom, for dark-brown Nohipalu Mustjärv and very turbid Lake Vôrtsjärv. For comparison with PP measurements the scalar irradiance data were used.

3.2 Estimation of the 1%–depth and constant irradiance depth

In general, there are two ways for determining the depths corresponding to 1% of irradiance just beneath the water surface ($z_{1\%}$) (the same for z_4). The first way consists of the downward irradiance measurements *in situ* or the model calculations, and finding the depths corresponding to these certain values of irradiance. Another possibility is to calculate these values by using the exponential law (Eqs. (3) and (4)) from known diffuse attenuation coefficient and subsurface PAR. Because the measurements of irradiance just below the surface (in an infinitesimal thin layer) are complicated we have used here only its modelled values.

As known, in natural water bodies $K_{d,\mathrm{PAR}}$ changes with depth irregularly according to vertical heterogeneity of optically active substances. A detailed investigation on the errors in underwater irradiance caused by using the averaged over depth $K_{d,\mathrm{PAR}}$ for calculations is presented in *Arst et al.* (2000). The vertical change of $K_{d,\mathrm{PAR}}$ is observed even in homogeneous water, the main reasons being very strong absorption in the violet and blue parts of the spectrum (mainly due to yellow substance) and also at the wavelengths exceeding 650 nm (due to the high absorption coefficient of water itself). Starting from some level the light corresponding to both ends of the PAR spectrum is practically totally absorbed. The remaining light corresponds to the wavelengths where the absorption coefficient is considerably smaller in comparison with that in the marginal regions of the PAR spectrum. We assumed the water body being optically homogeneous, thus, we investigated the vertical change of diffuse attenuation coefficient caused mainly by variation of spectral composition of light with depth. For the reasons described above we investigated also the spectral distribution of $z_{1\%}$ in different water bodies.

The spectral curves of $z_{1\%}(\lambda)$ calculated by Eq. (3) are shown in Fig. 1. The wavelength corresponding to the maximal value of $z_{1\%}$ increases with decreasing water transparency. Typically the values of $z_{1\%}(\lambda)$ in lakes are lowest (0.5–4 m) for the violet and blue part of the spectrum, while yellow light penetrates into deeper layers (3–12 m). Only in extremely clear lakes (Äntu Sinijärv) the euphotic depth in the blue region of the spectrum exceeds that in the red part; that is typical also for clear oceanic waters (*Jerlov*, 1976).

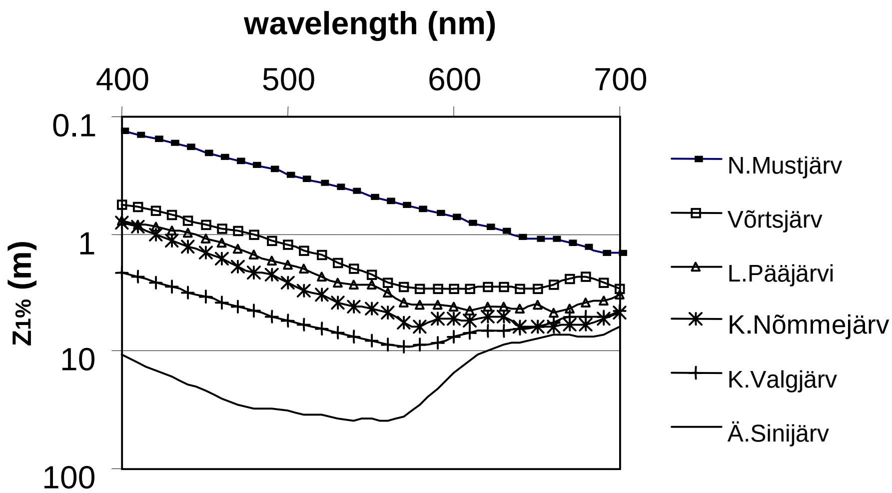

Fig. 1. Spectral variability of the 1%-depth, calculated from the data of diffuse attenuation coefficients taken from *Reinart and Herlevi* (1999). The names of the lakes are shown in the figure.

Using values of $K_d(\lambda)$ and the spectral incident irradiance calculated (in units μmol $s^{-1}m^{-2}nm^{1}$) by the model of *Bird and Riordan* (1986) for solar zenith angle 34.7° (58°N, summer solstice), the vertical distribution of $E_d(\lambda)$ was calculated by Eq. (2) at different depths in the water. After integration of the spectral values over PAR region the $E_{d,\mathrm{PAR}}(z)$ was obtained and $K_{d,\mathrm{PAR}}$ was estimated as described in "Methods". Now the two variants of $z_{1\%}$ were determined: (1) by vertical profiles of PAR in the water,

(2) by Eq. (3) using values of $K_{d,\mathrm{PAR}}$. For comparison the same procedure was performed for Jerlov's oceanic water type I.

In practice widely used exponential fit gives only approximate descripton of the decrease of $E_{d,PAR}$ with depth. In the upper layers of the water body $E_{d,PAR}$ decreases more rapidly than in lower layers, but these changes are different in different types of water bodies. To estimate how well the constant value of $K_{d,\mathrm{PAR}}$ suits to real attenuation, the $K_{d,\mathrm{PAR}}(z)$ at all depths was calculated down to $E_{d,\mathrm{PAR}} = 0.01 E_{d,\mathrm{PAR}}(z{=}-0)$ and relationship

$$K_{d,PAR}(z) = K_{d,PAR} + \Delta K \tag{5}$$

was found, where ΔK is difference between constant $K_{d,\mathrm{PAR}}$ (by exponential fit) and its real value at some depth z. These results are presented in Table 2. In this table also relative difference ε between maximal and minimal value of $K_{d,\mathrm{PAR}}(z)$ is shown, calculated as:

$$\varepsilon = \frac{K^{MAX}{}_{d,PAR}(z) - K^{MIN}{}_{d,PAR}(z)}{K_{d,PAR}}. \tag{6}$$

As seen, ΔK may be relatively big in the waters of Jerlov type I and Lake Äntu Sinijärv (accordingly 160% and 62%), which are most transparent, but also in lakes Nohipalu Mustjärv and Lammi Pääjärvi (87% and 48%), where maximum wavelength at 1% depth is shifted into red part of PAR (Table 3). Combined effect of averaging over depth and averaging over PAR induces that the result of exponential fit depends from data used for analysis.

Table 2. Values of constant $K_{d,\mathrm{PAR}}$ estimated by exponential fit of irradiance vs. depth down to 1%-depth, its averaged over depth difference from real attenuation value at any depth (Eq. (5)), ΔK, and standard deviation of ΔK. ε is relative difference between minimal and maximal value of $K_{d,\mathrm{PAR}}(z)$.

Water body	ε	$K_{d,\mathrm{PAR}}$ (m^{-1})	Average ΔK (m^{-1})	St.dev ΔK
N. Mustjärv	1.02	4.72	0.30	2.04
Vôrtsjärv	0.57	1.88	0.15	0.45
L. Pääjärvi	0.65	1.35	0.10	0.31
K. Nõmmejärv	0.73	0.88	0.06	0.22
K. Valgjärv	0.31	0.70	0.01	0.08
N. Valgjärv	0.42	0.51	0.01	0.07
Ä. Sinijärv	1.2	0.16	0.02	0.05
Jerlov I	6.61	0.023	0.002	0.02

Table 3. Values of 1%-depth and z_4 by different methods in water bodies.

Water body	Δλ of maximum $z_{1\%}$ (nm)	1%-depth (m)			Error of estimated $z_{1\%}$ applying Eq. (3)	depth of irradince 4 μmol $s^{-1}m^{-2}$ (m)	
		Maximum spectral $z_{1\%}(\Delta\lambda)$	From $E_{d,\mathrm{PAR}}(z)$ curve	4.6/ $K_{d,\mathrm{PAR}}$		From $E_{d,\mathrm{PAR}}(z)$ curve	By Eq. (4)
N. Mustjärv	~700	1.27	0.90	0.96	6.7%	1.35	1.31
Vôrtsjärv	580–640	2.93	2.31	2.45	6.0%	3.4	3.2
L. Pääjärvi	610–640	4.23	3.2	3.4	6.3%	4.8	4.5
K. Nõmmejärv	580–590	6.21	4.91	5.22	6.3%	6.7	6.4
K. Valgjärv	570–580	9.07	6.5	6.59	1.5%	9.0	8.6
N. Valgjärv	540–560	12.3	8.92	9.07	1.7%	12.2	11.8
Ä. Sinijärv	540–560	39	27	29	7.4%	39.0	36.1
Jerlov I	460–470	263	174	196	13 %	231	212

Because usually the measurements of $E_{d,\mathrm{PAR}}(z)$ are performed at certain depths, we calculated additionally the values of $K_{d,\mathrm{PAR}}$ by exponential fit varying the depth of lowest measurements point around $z_{1\%}$ ±0.25 m. The corresponding variation of $K_{d,PAR}$ caused maximum error ±3% of estimated $z_{1\%}$ in extremely dark Nohipalu Mustjärv, but in all other cases it was less than 2%. The values of $z_{1\%}$, estimated from vertical profiles of underwater irradiance, and by Eq. (3) are presented in Table 3.

These results show that in optically homogeneous water bodies the value of $z_{1\%}$ determined as $4.6/K_d$ systematically exceeds the true value of $z_{1\%}$. The reason is that the regression line of irradiance vs. depth data gives us the underestimated value of subsurface irradiance, which is not taken into account when using the constant 4.6 for determining $z_{1\%}$ (*Arst et al.,* 2000). However, the relative difference of these two $z_{1\%}$ values is not big, 2–13%, being maximal for very clear waters (Jerlov I, Lake Äntu Sinijärv). This error accords very well with parameter ε: bigger variation of $K_{d,\mathrm{PAR}}(z)$ causes the bigger error in applying of Eq. (3) for calculating the euphotic depth. In real measurements under natural conditions at the 1%-level the radiation values are low and often measured with relative error 10–20%. Thus, the estimation of $z_{1\%}$ through the mean attenuation coefficient $K_{d,\mathrm{PAR}}$ gives in most cases rather satisfying results, being a useful method especially when *in situ* radiation measurements near 1% depth are hampered.

The relative difference between the maximal spectral value of $z_{1\%}(\lambda)$ and $z_{1\%}$ is biggest in clear waters (51% in type I by Jerlov) and decreases with the increasing of the water turbidity and colour (26–41% in lakes). However, these differences are remarkable and one has to be careful using measuring devices with different spectral response for estimation of the euphotic depth by optical methods.

Analysing the results of z_4 presented in Table 3, we found that the application of the exponential vertical decrease of PAR (i.e. using of Eq. (4)) leads to the systematic underestimation of z_4 comparing with that obtained by integrating the spectral values over PAR at different depths. The reason is that the real attenuation of irradiance at deep layers is less than attenuation in upper water column. However, this underestimation (3–8%) may be even less than expectable measurements errors in the z_4-depth. Consequently, the small values of PAR in the water (by our estimations below 25 μmols^{-1}m^{-2}) can be satisfactorily estimated using the diffuse attenuation coefficient averaged for depth and PAR.

3.3 The relationship between the depth of constant irradiance z_4 and 1%-depth

From Eqs. (3) and (4) we obtain:

$$\frac{z_4}{z_{1\%}} = 0.22\ln\left[E_{d,0,PAR}(z=-0)\right] - 0.30\,, \tag{7}$$

where $E_{d,0,\mathrm{PAR}}$ are in units μmol s^{-1} m^{-2} and $z_{1\%}$ and z_4 in meters. It shows, that there cannot be a universal correlative relationship between $z_{1\%}$ and z_4, because the values of z_4 (and consequently the ratio $z_4/z_{1\%}$) depend on the values of subsurface irradiance.

We investigated the variations of euphotic depth criteria $z_{1\%}$ and z_4 in different light conditions by means of model calculations. The dependence of the diffuse attenuation coefficient on the solar zenith angle was taken into account according to *Kirk* (1981):

$$K_d = \frac{1}{\cos\varphi}\left[a^2 + (0.425\cos\varphi - 0.190)ab\right]^{0.5}, \tag{8}$$

where K_d is the average value of the spectral diffuse attenuation coefficient over the 1%-layer, φ is the angle of the direct solar beam to the vertical just below the water surface (after refraction), a and b are the spectral absorption and scattering coefficients.

Necessary values of absorption and scattering coefficients we calculated following the formulas by *Gordon and Morel* (1983) and *Bricaud et al.* (1995), which allow to determine a and b relying on the chlorophyll a concentration. This was assumed to be C_{Chl} = 10 mg/m^3. The values of incident spectral solar radiation and PAR were determined according to the model of *Bird and Riordan* (1986). Incident radiation in the conditions of a clear sky was calculated for equatorial and polar areas (5°N and 85°N, respectively) and for 58°N at the equinox and summer solstice. The maximum zenith angle was taken to be 80°. Variation of $z_{1\%}$ and z_4 due to the latitude and season is shown in Fig. 2. The difference between $z_{1\%}$ and z_4 during the day is biggest at noon and increases with decreasing latitude. Except for early morning and late evening, $z_{1\%}$ is greater than z_4. As follows from Eq. (7) the differences between $z_{1\%}$ and z_4 depend also from local sky conditions (cloudiness) which remarkably changes the incident irradiance.

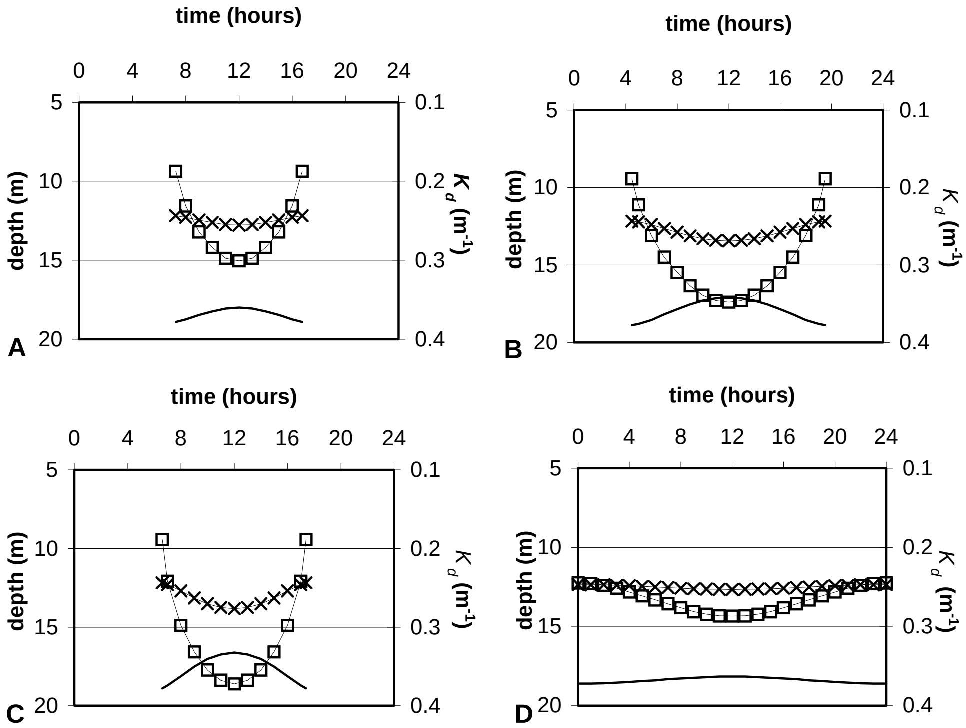

Fig. 2. Diurnal variation (by model calculations) of the diffuse attenuation coefficient $K_{d,\mathrm{PAR}}$ (line), 1%-depth $z_{1\%}$ (crosses) and depth z_4 (empty squares) at 58°N at equinox (A) and summer solstice (B); latitude 5°N (C) and latitude 85°N (D) at summer solstice for water with C_{chl}=10 mg l^{-3}.

3.4 *The optical criteria of euphotic depth in Estonian and Finnish lakes*

We computed the relationship $z_4/z_{1\%}$ also using the data obtained for Estonian and Finnish lakes. Surprisingly we got a rather strong relationship: $z_4 = 1.25z_{1\%}$ with the correlation coefficient of 0.99 (this and the following correlation coefficients were significant at the $p < 0.01$ level). By measurements the $z_4/z_{1\%}$ ratio was usually 1.2–1.3, with the minimum of 0.9 and maximum of 1.36. Using the downwelling irradiance data, *Adamenko et al.* (1991) got a regression line similar to ours with the coefficient of 1.24. The explanation of this good correlation is that our measurements were all carried out in summer, nearly at noon, in a region between 57° and 62°N and mostly under good weather conditions i.e. in Eq. (5) $E_{d,0,\mathrm{PAR}}$≈const for the present data set (if to compare the values of z_4 and $z_{1\%}$ in Fig.2B between 10 and 14 o'clock there also will be a good correlation).

The results obtained for the Estonian and Finnish lakes showed $z_{1\%}$ varying from 0.4 to 21.9 m (Fig. 3) and z_4 from 0.5 to 29.6 m. The scalar irradiance at the depth $z_{1\%}$ varied between 4.2 and 28.3 μmol s^{-1}m^{-2}, the average value being 16.2 μmol s^{-1} m^{-2}.

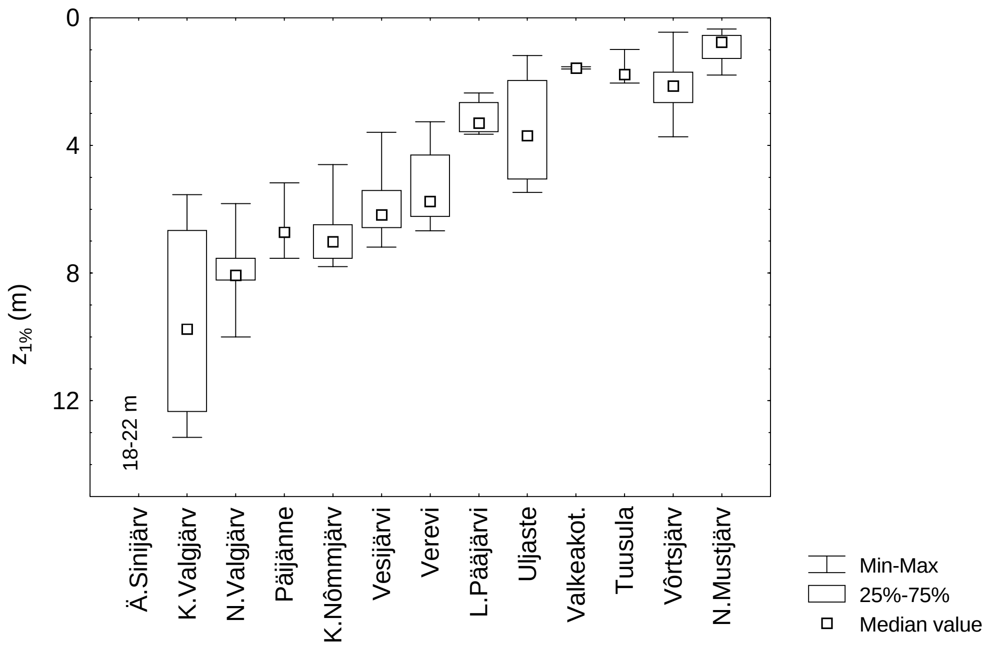

Fig. 3. Euphotic depth for different Estonian and Finnish lakes estimated as $z_{1\%}=4.6/K_{d,\mathrm{PAR}}$. The names of the lakes are shown in figure.

3.5 The primary production in the euphotic zone and the depth of the compensation point

We analysed the values of z_4 and $z_{1\%}$ also together with the vertical profiles of photosynthesis in our lakes. In the measured depth profiles a notable decrease in the rate of phytoplankton photosynthesis is commonly observed near the surface (some examples in Fig. 4). With increasing depth and diminishing irradiance, photoinhibition is reduced and the maximum rate of photosynthesis is achieved. With a further increase in depth, irradiance decreases to the point at which light becomes limiting for photosynthesis, and primary production diminishes approximately exponentially with depth and linearly with irradiance.

Maximum and integral primary productions ($PP_{\max}$ and PP_{int}) varied from 0.24 to 107 mg C m^{-3} h^{-1} and from 0.177 to 112 mg C m^{-2} h^{-1}, respectively, being highest in Lake Võrtsjärv and very low in lakes Äntu Sinijärv and Nohipalu Mustjärv (Table 1). We could find low $PP_{\max}$ values (<10 mg C m^{-3} h^{-1}) in most of the lakes, only in Lake Võrtsjärv $PP_{\max}$ was permanently high (35 to 107 mg C m^{-3} h^{-1}).

The zero-level of primary production was estimated in two ways: 1) by linear extrapolation of PP^* vs. E_0 to zero; 2) by exponential decreasing of PP^* down to 0.1% of $PP_{\max}$. We preferred the calculation by the linear extrapolation because this gives more rigorous results than the exponential extrapolation, which is very sensitive to small errors in the input data. The correlation between the values of $z_{PP=0}$ obtained by these two methods was high (R= 0.97).

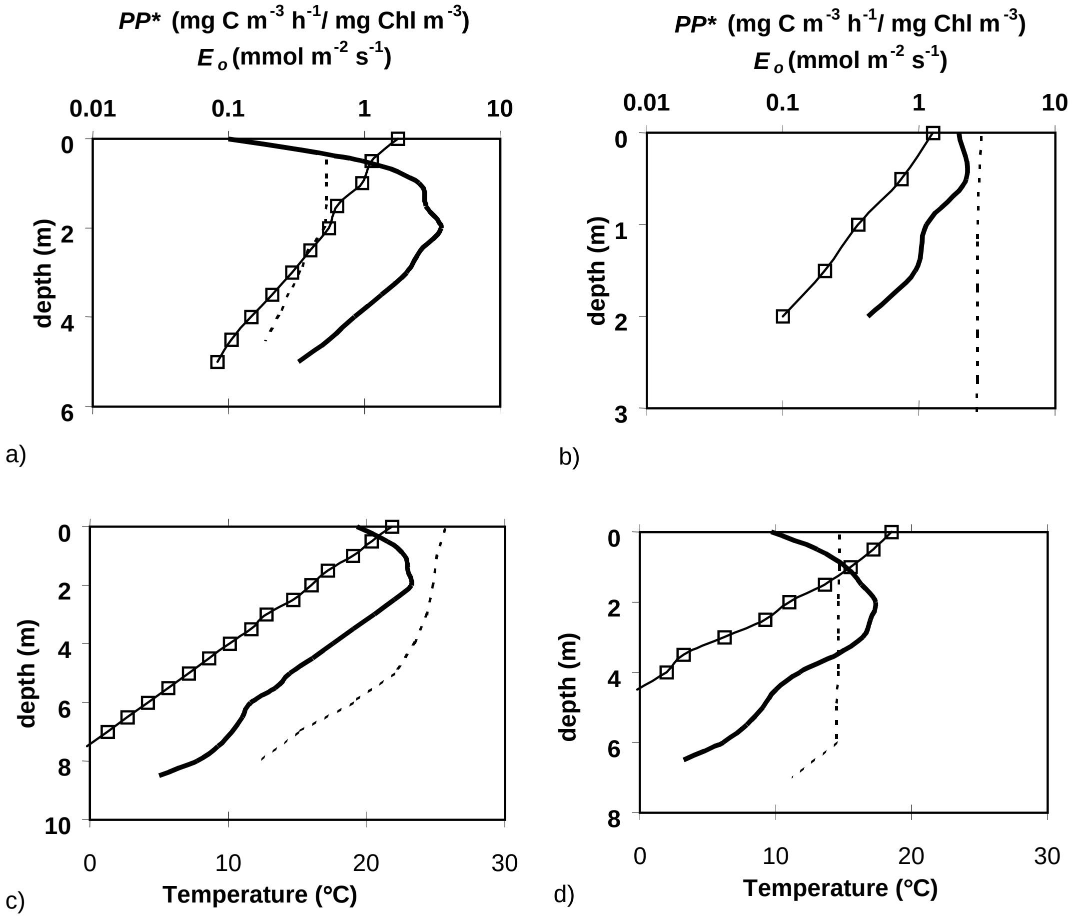

Fig. 4. Vertical distribution of specific primary production *PP** (thick line) and irradiance $E_{0,PAR}$ (squares) in some Estonian lakes: a) Kurtna Nômmejärv 07/06/96, b) Vôrtsjärv 05/08/97, c) Koorküla Valgjärv 21/08/96, d) Nohipalu Valgjärv 18/09/96. Temperature profiles are by dotted line.

The values of $E_{0,\mathrm{PAR}}$ at the depth $z_{\mathrm{PP}=0}$ were in the limits of 1–80 μmol $s^{-1}m^{-2}$ (average 14.3 μmol $s^{-1}m^{-2}$) which is 0.1–2.8% (average 1.2%) of the subsurface irradiance. The values of the compensation depth, z_{comp}, were computed as described before. Irradiance at the compensation depth, E_{comp} varied from 5.6 to 530 μmol $s^{-1}m^{-2}$, forming 0.4–53% of the subsurface irradiance.

The next step was to investigate the correlation's between $z_{\mathrm{PP}=0}$, $z_{1\%}$, z_4 and z_{comp} The correlation $z_{\mathrm{PP}=0}$ vs. $z_{1\%}$ is shown in Fig. 5a and the correlation z_{comp} vs. $z_{1\%}$ in Fig. 5b. For the parameters under investigations we obtained the following regression formulae (R is correlation coefficient; N is the number of cases, p<0.01):

$z_{\mathrm{PP}=0} = 1.04z_{1\%}$	R = 0.84	N = 41	std.error 1.2 (m),
$z_{\mathrm{PP}=0} = 0.84z_4$	R = 0.83	N = 41	std.error 1.2 (m),
$z_{\mathrm{PP}=0} = 2.03\ z_{\mathrm{comp}}$	R = 0.60	N = 29	std.error 2.1 (m),
$z_{\mathrm{comp}} = 0.17z_{1\%} + 1.65$	R = 0.41	N = 29;	std.error 0.95 (m),
$z_{\mathrm{comp}} = 0.15z_4 + 1.61$	R = 0.45	N = 29;	std.error 0.93 (m).

Transparency by Secchi depth, z_{Secchi} varied between 0.15 and 5.8 m, when $K_{0,\mathrm{PAR}}$ is between 0.35–10.1 m^{-1}. The proportion of incident light reaching the depth of z_{Secchi} is commonly in the range between 5 and 15% (*Tilzer*, 1989). Because of differing the lakes by properties of absorption and scattering, levels at the depth z_{Secchi} in these lakes differ too. In turbid Lake Võrtsjärv the value of PAR at the depth z_{Secchi} can be up to 58% from subsurface light, while in relatively clear Lake N. Valgjärv about 2%.

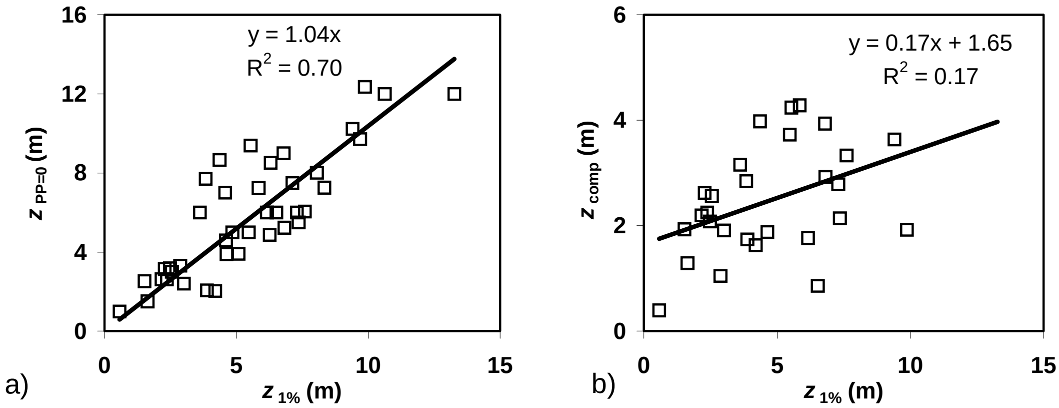

Fig. 5. Relationship of the euphotic depth $z_{1\%}$ (a) to depth of zero primary production $z_{PP=0}$ and (b) to depth of the compensation point z_{comp}.

Above mentioned criteria of euphotic depth are related to z_{Secchi} by following expessions:

$z_{1\%} = 1.6 z_{\mathrm{Secchi}}$	R = 0.82	N = 41	std.error 1.4 (m),
$z_4 = 0.84 z_{\mathrm{Secchi}}$	R = 0.80	N = 41	std.error 2.0 (m),
$z_{PP=0} = 1.96 z_{\mathrm{Secchi}}$	R = 0.56	N = 29	std.error 1.8 (m),
$z_{\mathrm{comp}} = 0.3 z_{\mathrm{SecciD}} + 1.95$	R = 0.40	N = 29;	std.error 0.90 (m).

These results show that the data of Secchi depth are insufficient for determining the light levels in different lakes for photosynthesis studies and in situ PAR measurements are appreciated.

The correlation coefficients for the compensation point are much lower than those for the other parameters. This is logical as the primary production depends directly on the light entering the water and phytoplankton reacts quickly (~15 min) to the changes in light, but respiration is affected mostly by concentration of phytoplankton and temperature and its dependence on $E_{0,\mathrm{PAR}}$ is indirect (*Giorgio and Peters*, 1993).

The value of E_{comp} (Table 4) is subject to large uncertainty as there has been not taken account the loss of photosynthetically produced organic C due to processes other than phytoplankton respiration (release of dissolved organic material, grazing, etc.). On the basis of these data we can not suggest any constant value for E_{comp} in all our lakes;

on the contrary, it can be very different, depending from species compositions, chemical properties and temperature in these lakes.

Table 4. Average, minimum and maximum percentages of subsurface scalar irradiance $E_{0,PAR}$ (μmol $s^{-1}m^{-2}$) at different depths important for photosynthesis computed using the data for six Estonian lakes in 1995–97.

	$E_0(z_4)/E_0$, %	$E_0(z_{Secchi})/E_0$, %	$E_0(z_{PP=0})/E_0$, %	$E_0(z_{comp})/E_0$, %
AVERAGE	0.5	14.6	1.2	13.2
MINIMUM	0.2	2.0	0.1	0.4
MAXIMUM	1.9	58.4	2.8	53.4

These results show that in our measurement conditions the value of $z_{1\%}$ corresponds well to the level, where primary production approaches zero. Correspondence is a little worse for constant irradiance depth z_4 (remember that these z_4 values are slightly underestimated). However, our experimental; data are insufficient to decide which criterion, $z_{1\%}$ or some depth of constant irradiance (instead of 4 μmol $s^{-1}m^{-2}$ there may be some other value), is more suitable for describing the depth of zero primary production, including its daily variation.

3.6 Mixed depth and critical depth of photosynthesis

However the thickness of the layer where light, temperature and nutrient conditions are suitable for the photosynthesis depends also from vertical mixing of water, which in natural conditions moves the phytoplankton through variable light field. We did not take into account the mixing of water and samples for PP estimations are obtained at fixed depths. In reality phytoplankton is not exposed to the same value of light for very long time. This avoids photoinhibition close the surface, but in deeper layers the PAR is too low for photosynthesis. The depth of mixed layer z_{mixed} could be determined by vertical profile of temperature measurements (examples in Fig. 4).

Typical to shallow lakes (Võrtsjärv, K, Nõmmejärv and Uljaste) is that during summer their water is well mixed over whole water column, even when measurements depth exceeds the average depth of lake. The mixed layer depth in deeper lakes is determined by local climatic conditions, and it was quite similar for lakes in the region under investigation (Table 5). By our estimations it increases towards the end of summer, but we had only few data on the thermal regime of these lakes. If the depth of mixed layer increases, the average PAR in this layer decreases and consequently the total rate of photosynthesis by the whole phytoplankton population throughout the water column should decrease. There exists a critical depth of mixed layer beyond which respiratory carbon loss exceeds photosynthetic carbon gain. Thus when $z_{mixed}>z_{critical}$ the vertically integrated rate of phytoplankton photosynthesis is less than that needed to keep pace with respiratory consumption of organic C and growth of phytoplankton biomass can not occur. The $z_{critical}$ can be very shallow if there is: 1) the high attenuation of PAR in water; 2) high light requirement by phytoplankton for saturation of photosynthesis; and 3) very low irradiance values at cold season on higher latitudes.

Table 5. Values of different depths (m) related with photosynthesis in water. (Explanations in text.)

Lake	$z_{1\%}$(measured)	$z_{pp=0}$	z_{comp}	z_{mixed}	$z_{critical}$
N.Mustjärv	1.3	–	–	1	–
Ä.Sinijärv	21.9	–	–	4.5	–
K. Nõmmejärv	4.6–7.8	4.5–7.6	2.9–3.3	3.0–4.5	4.7–8.2
Uljaste	2.7–5.5	4.1–6.2	1–1.9	2.2–4.5	1.8–4.0
N.Valgjärv	5.8–10.6	–	–	3.0–6.0	–
K.Valgjärv	5.5–13.1	6.6–11.6	1.9–4.2	4.5–7.0	6.5–27.2
Verevi*	3.8–6.7	5.5–9.3	0.9–4.6	2.2–5.0	6.3–13.7
Võrtsjärv	0.4–3.4	1.2–4.7	0.4–2.6	2.8–4.5	1.3–13.4

*optical measurements only in upper 4 m layer.

Approximate expression for critical depth, first derived by *Sverdrup* (1953) and modified by *Nelson and Smith* (1991) is:

$$z_{critical} = \frac{A\overline{E_{d,PAR}(z=0+)}}{K_{d,PAR}E_{comp}}. \tag{9}$$

It shows the dependence of $z_{critical}$ on time-averaged irradiance at the surface, $E_{d,\mathrm{PAR}}(z=0+)$, $K_{d,\mathrm{PAR}}$ and irradiance at the compensation point E_{comp}. The coefficient A takes into account the loss of irradiance due to surface reflectance, averaging period of $E_{d,\mathrm{PAR}}(z=0+)$, and specifications of devices. Using the subsurface PAR values, we can avoid from uncertainties due to surface reflectance and relative part of PAR in total irradiance. Daily average value of PAR is estimated by measured around noon $E_{0,\mathrm{PAR}}(z=-0)$, taking into account its sinusoidal variation. Variation of average $K_{d,\mathrm{PAR}}$ during day is remarkable only in conditions of low sun and therefore its value measured around noon could be used. If irradiance is in units µmol s^{-1} m^{-2} then A=0.65.

From May to August the values of $z_{critical}$ have been typically higher than z_{mixed} (Table 5), which is supporting phytoplankton growth (it could be seen also by increasing of C_{chl} throughout summer in most of lakes). Only few primary production measurements are made in autumn. They show that z_{mixed} exceeds $z_{critical}$, the growth of phytoplanton is light limited and then biomass decreases. Therefore the variations of mixed and critical depths of photosynthesis, and average lightening of mixed layer have to taken into account studying PP in lakes where water is vertically stratified (usually deep lakes) or annual change of PP is of interest.

4. *Conclusions*

1. The application of the exponential vertical decrease of light in the PAR region may lead to considerable errors in the study of the clear or optically strongly stratified

water bodies, but in turbid waters these errors may not always be observed. In coastal waters and lakes the values of $z_{1\%}$, calculated through the mean attenuation coefficient $K_{d,0}$ are rather close to its real values. The mean $K_{d,0}$ can be used for the estimation of the $E_{d,0}$ values up to 1% of subsurface PAR irradiance, as errors by measurements and calculations are in same magnitude.

2. In general, two optical criteria, $z_{1\%}$ level and a constant value of PAR, cannot give a good correlation for data complex obtained in strongly different light conditions. However, our experimental results show a strong relationship between these two criteria ($z_4/z_{1\%} = 1.25$) for the data set obtained for Estonian and Finnish lakes. The reason is that our measurements are carried out mostly in clear weather around noon at summer (PAR varies in rather narrow limits).
3. The proportion of subsurface PAR reaching the Secchi depth varies between 2% in clear lakes and 58% in turbid lakes. Attempts to equalise light levels using the Secchi depths data for photosynthesis experiments in different lakes seems to offer only little advantage over constant incubation depths.
4. The optical criteria of euphotic depth describe the zone of positive gross primary production rather than the zone of positive net production. We did not find any certain irradiance value always corresponding to the zero level of primary production or compensation point. According to the primary production measurements in our lakes, the compensation point was placed at the depth, which is reached by 13% of subsurface irradiance in the PAR region; the depth $z_{pp=0}$ received 1.2% of subsurface light. The depth $z_{1\%}$, widely used in practice, corresponds rather well to the level where primary production approaches zero ($z_{PP=0} = 1.04\ z_{1\%}$).
5. The connections between different criteria of euphotic depth and primary production were determined without taking into account the vertical mixing of water. By our results in most cases the mixing depth of water does not exceed the critical depth of photosynthesis during summer period. However studying primary production in vertically stratified lakes and its annual change one have to pay attention to the variations of mixed and critical depths.

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