

Photoautotrophic Productivity in Eutrophic Ecosystems

9

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Abstract

Enhanced photoautotrophic productivity of lakes, reservoirs, rivers and streams is a consequence of prolific nutrient loading from the catchment known as eutrophication. In most cases, it is a syndrome of ecosystem responses to human activities in the watershed. Primary production is strongly influenced by latitude, insolation and nutrient availability, but also depends on lake size, the size of the catchment, the type of water body and lake depth. The outcome is therefore highly variable for specific continental waters. Nevertheless, autotrophic production is perhaps the best parameter to define the trophic level of waters. The complex techniques and frequent measurements necessary to estimate production accurately hampered the application, however. Recent improvements in methods and new developments in monitoring strategies have revived interest in primary production as an index to define trophic level. Important relationships of production to environmental variables are analysed. Then, development of boundary criteria are discussed, production indices compared and trophic boundary classifications compiled from different authors. Maximum and global production is emphasised. The impact of a warmer world as a consequence of climate change on continental waters is highlighted and future perspectives of photoautotrophic production summarised.

Keywords

Productivity · Continental waters · Eutrophication · Trophic indices · WFD

9.1 Introduction

Eutrophication is the process of increased productivity of lakes, rivers and estuaries as a consequence of increased nutrient input from the water shed. The process of eutrophication can be natural but is in most cases a syndrome of ecosystem responses to human activities in the catchment. Accordingly, production of plants, bacteria and animals usually increase but the outcome is highly variable. Phytoplank-

ton primary production is strongly influenced by latitude (Brylinsky and Mann 1973; Bouillon 2003), insolation (e.g. Jónasson 1974; Anderson 1974) and nutrient availability (e.g. Schindler 1978), but also depends on lake size, the size of the catchment, the type of water body and lake depth (Fee 1979, 1980; Knoll et al. 2003; Nöges 2009).

Primary production is a fundamental ecological variable. It is a measure of the extent to which primary energy input by solar energy to the aquatic environment is transformed and accumulated into biological entities adding organic substance to the ecological sphere. Because production is defined as the flux of inorganic carbon into autotrophic organisms per unit time, this rate can be used as an indicator of growth and hence as a major criterion to determine the

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trophic state of a water body. Trophic categorization based on phytoplankton productivity, however, is based on the assumption that inputs from littoral or allochthonous sources are negligible. On a global basis, productivity from the littoral or of external origin can be much larger than phytoplankton production in many cases (Wetzel 1990).

The original concept of the trophic system aims to arrange surface waters, regardless of their size and ecological characteristics, in a continuous sequence of increasing trophic. The basis for comparison is the intensity of organic production (Ohle 1958). The autotrophic capacity of a lake or a river therefore appears to be an ideal basis for establishing an absolute scale of trophic level (Elster 1954, 1958; Winberg 1960). Hence, 'trophism' is often directly equated with the intensity of primary production, which should better be termed 'autotrophic production' following argumentation by Flynn (1988).

The aim of this chapter is to gather and critically evaluate information on the use of primary production criteria to define trophic boundary conditions, particularly for variable eutrophic systems.

9.2 Lakes, Data and Methods

The lakes covered in this study range from ultra-oligotrophic Arctic lakes to hypertrophic tropical lakes, include shallow and deep lakes, high mountains and flatland lakes from around the world. If not otherwise stated, the data used in this compilation are original or come from information summarised in Dokulil (2005) for alpine lakes, Dokulil et al. (2005) for a variety of lake types, Håkanson and Boulion (2001) for lakes from the former Soviet Union (their Annex A) and Kimmel et al. (1990) for reservoirs.

Carbon uptake can conveniently be estimated using the ^{14}C -technique developed by Steemann Nielsen (1951) or one of its modifications (Dokulil and Kaiblinger 2009). Incubation periods of equal or less than 2 h are considered to represent gross uptake. Alternatively, photosynthetic oxygen evolution or fluorescence signals can be measured (Dokulil et al. 2005; Dokulil and Kaiblinger 2009). For details on methods and conversions to carbon, refer to Wetzel and Likens (1991, p. 207 ff.) and Kaiblinger and Dokulil (2006).

Chlorophyll-a (chl-a) is used here as a universal indicator of algal biomass and was measured by extraction in either acetone or ethanol followed by photometrical determination (Lorenzen 1967, ISO 10260 1992).

Production estimations reported as oxygen rates were converted to carbon using a factor of 0.3 mg C per mg O_2 assuming an assimilation coefficient of 1.25. Hourly rates of photosynthesis were converted to daily rates using appropriate day length conversion (day light hours \times 0.6; Talling 1957).

9.3 Primary Productivity Relationships

Almost all definitions of trophic categories are primarily related to nutrient concentration and loading from the catchment (Rast and Thornton 2005). Klapper (1992) related average annual integrated primary production (ΣSP) to total phosphorus (TP) concentration at spring overturn (Fig. 9.1).

A similar relation to soluble reactive phosphorus at spring overturn (SRP_{SP}) was reported by Fricker (1981). Daily and annual production was correlated with TP, SRP_{SP} and to TP concentrations predicted from models (Clasen and Bernhardt 1980; Fricker 1980; Vollenweider and Kerekes 1980; OECD 1982). Håkanson and Boulion (2001) have related TP to maximum and mean volumetric daily production in their extensive study, trophic relations. Similarly, production estimates from clear and humic lakes were correlated to chl-a and TP by Nürnberg and Shaw (1999). A recent meta-analysis examined the effects of several variables including nutrients on absolute and relative production estimates (Faithfull et al. 2011). One of their conclusions was that both P and N can be predictors of primary production. This well-established, positive relationship between loading and productivity becomes apparent when phytoplankton biomass increases as a consequence of eutrophication (e.g. Harper 1992). Eutrophic and hypereutrophic lakes can sustain very high algal biomass often dominated by few taxa. In such systems, however, total phytoplankton biomass as well as all groups except blue-greens and diatoms tend to flatten off (Watson et al. 1992, 1997). This curvilinearity is also evident during the oligotrophication process (Jeppesen et al. 2005). Phytoplankton biomass can be estimated indirectly using chl-a as a surrogate parameter. Both variables correlate well as has been demonstrated many times (e.g. Huot et al. 2007). The chl-a therefore remains the best proxy of phytoplankton biomass for studies of primary productivity (Huot et al. 2007).

The chl-a correlates with daily photoautotrophic production (A) over a wide range of trophic levels from ultra-oligotrophic arctic lakes to highly productive tropical lakes in Africa (Fig. 9.2).

Average volumetric production in the euphotic zone directly depends on mean chl-a concentration. The correlation of the 214 observations is highly significant ($r^2=0.81$, $p<0.001$). The 95% confidence limits remain narrow over the entire range (4 orders of magnitude) indicating good agreement between variables. This close relation allows designation of empirical trophic boundaries (Fig. 9.2). These boundaries omit average values as suggested by the regression equation and is orientated towards accommodation of all production rates in each trophic category.

To model photoautotrophic production from chl-a (Håkanson and Peters 1995; Bot and Colijn 1996; Morin et al. 1999), additional information on the relationship with incoming radiation is required. Daily column production

Fig. 9.1 Fitting annual primary production to spring total phosphorus concentration. The equation, 95% confidence limits (C.L.) and approximate trophic delineation are given in the diagram. (Modified from Klapper 1992)

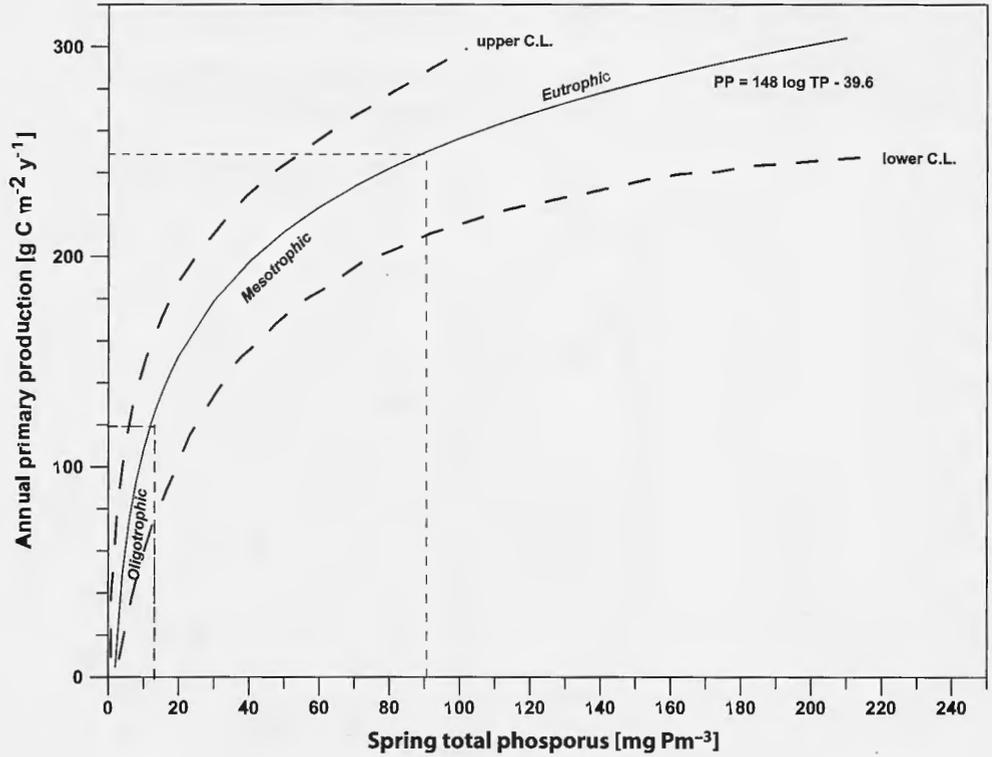


Fig. 9.2 Dependence of average daily euphotic zone production rate (A) on chl-a using data from Kimmel et al. 1990; Håkanson and Boulion 2001; Dokulil 2005 and Dokulil et al. 2005. Log-log plot. The equation, statistical data and 95% C.L. and trophic boundaries are inserted in the diagram

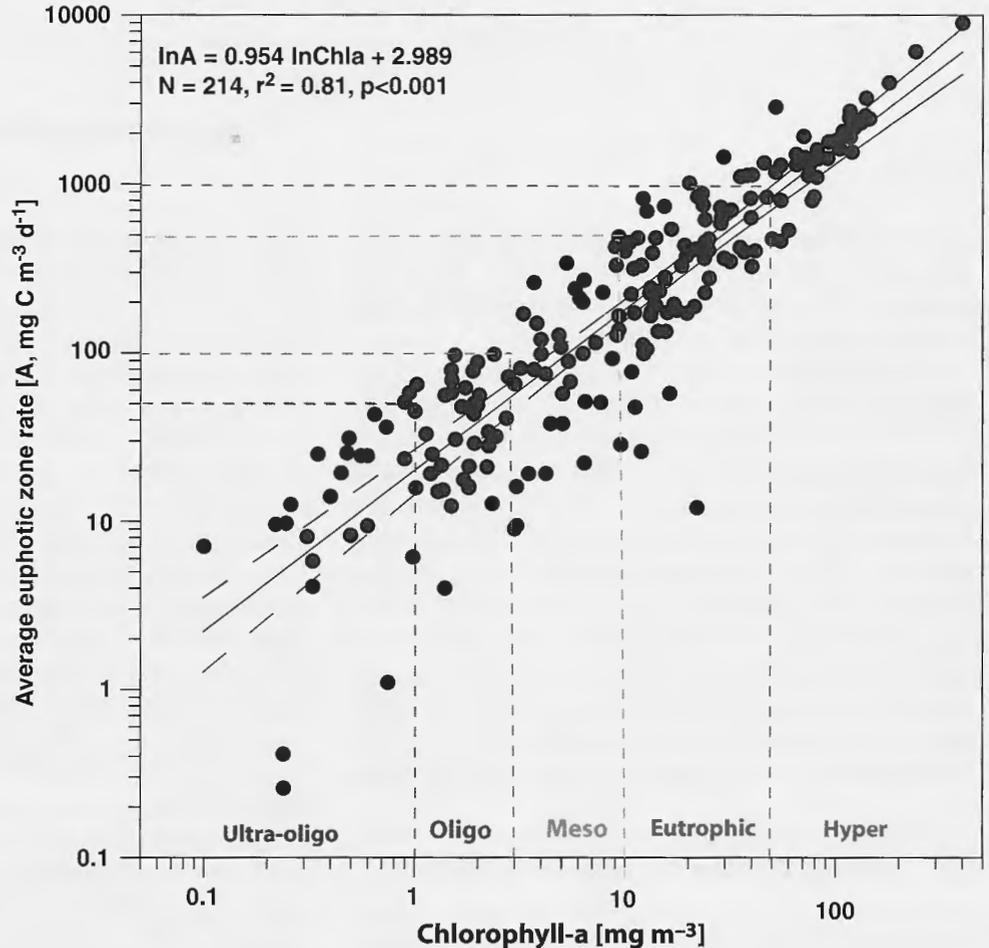
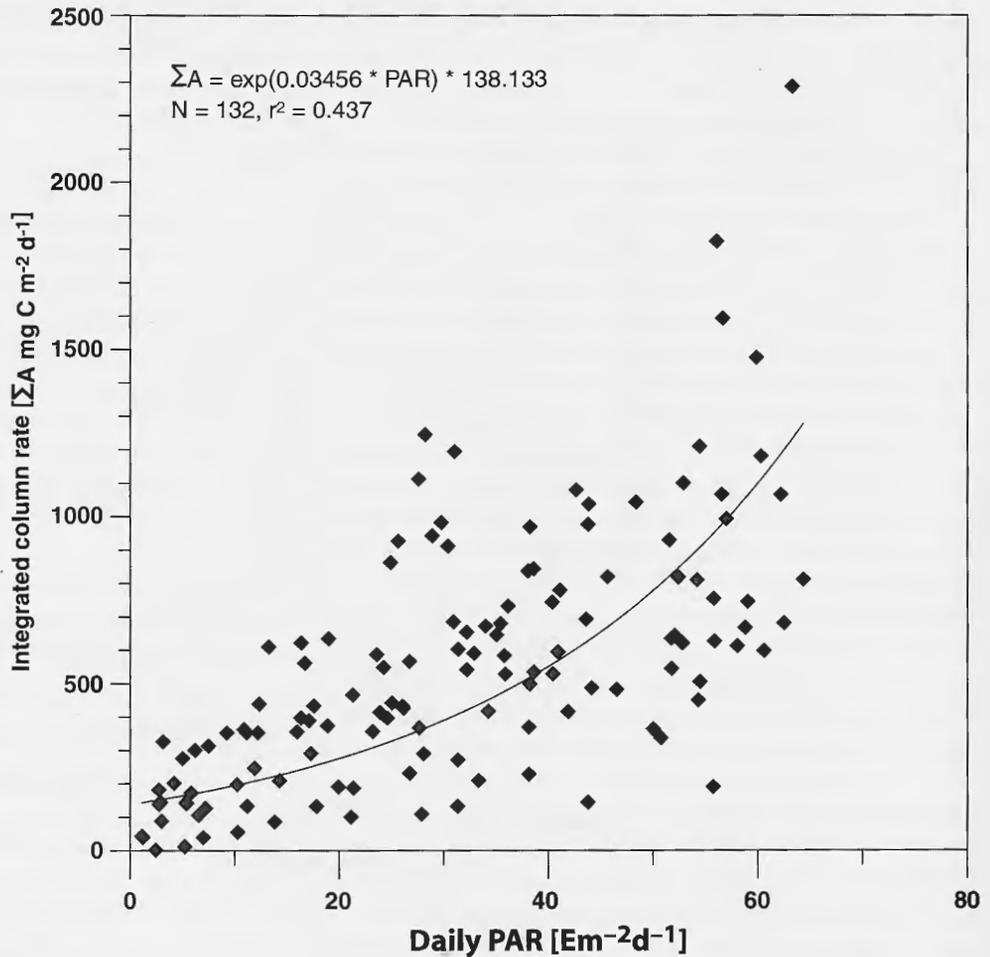


Fig. 9.3 Daily integrated column production related to daily insolation as photosynthetic active radiation (PAR) using data from Kabas 2004



(ΣA) correlated with daily photosynthetic available radiation (PAR) in an urban lake in Vienna, Austria (Fig. 9.2). Jónason et al. (1974) reported significant correlation of annual average production to solar radiation (Fig. 9.3).

In a turbid lake, ΣA was more loosely related to PAR because of highly variable underwater light attenuation (Lind et al. 1992). As a further consequence of this light relationship, production estimates were significantly linked with latitude (Brylinsky and Mann 1973; Nürnberg and Shaw 1999; Håkanson and Boulion 2001; Faithfull et al. 2011). Although regulation of ΣA by latitude alone is unlikely, as much as 50–74% of the variability of ΣA is explained by latitude. The ΣA rate has also been shown to be highly dependent on watershed land use in a reservoir study by Knoll et al. (2003) while production at the best depth (A_{opt}) correlated significantly with chl-a and TP. From these data, the authors conclude that land use sets an upper limit to primary production.

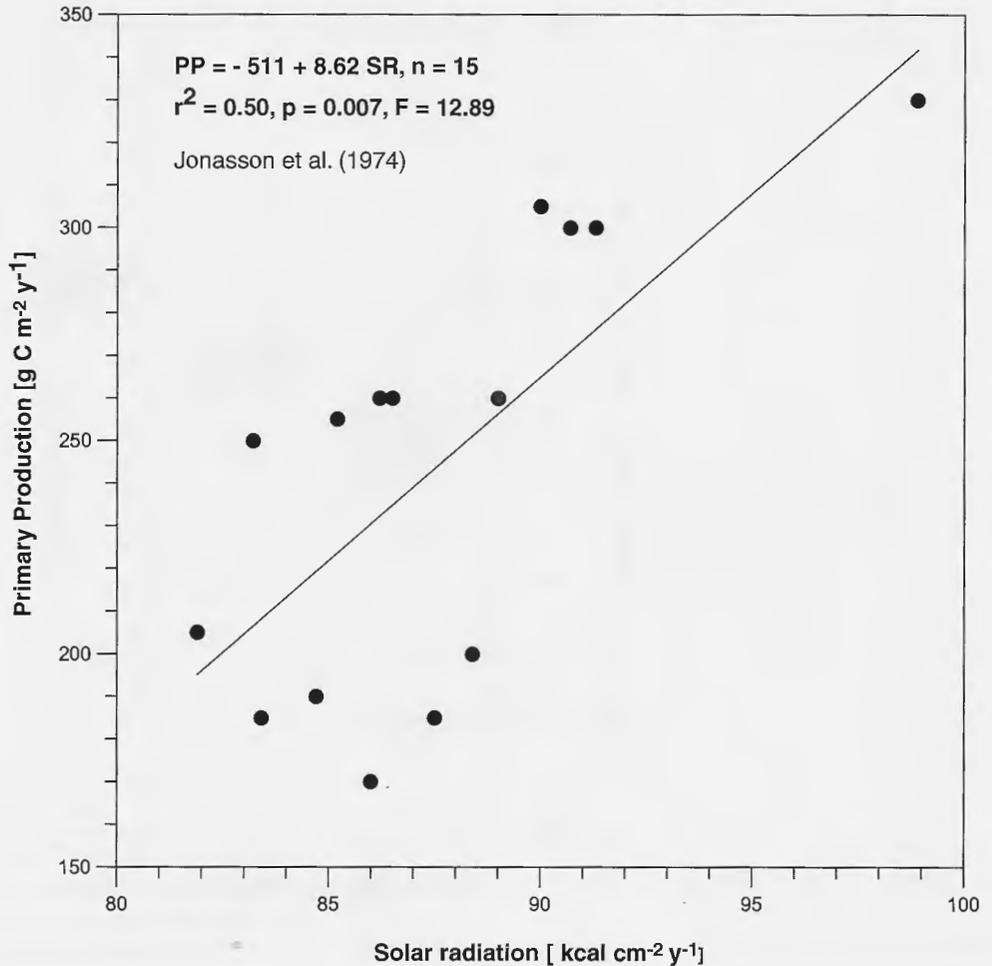
9.4 Developing Trophic Boundary Criteria

Vollenweider (1968) considered it difficult to suggest a simple unequivocal correlation between production capacity and trophic level. One of his basic concerns was the correct

choice of reference values and their space and time dimensions used for comparison. A logic option is the annual carbon uptake per unit surface area ($\Sigma\Sigma P$), which allows comparison of lakes and also to relate them to other ecological units such as estimates of terrestrial or marine primary production (Geider et al. 2001). Complications, however, arise from the large variability of lake size and depth affecting not only the amount of production rates but also the shape of the depth profile. Variable underwater light attenuation owing to external factors or feedback mechanisms as a consequence of increasing algal abundance during eutrophication additionally influences column production per square metre. Moreover, complex and time-consuming methodology further hampered the application of photosynthetic rate measurements to define trophic situations. As a consequence of these difficulties, other variables became more popular as indicators to define boundaries of trophic categories (see e.g. OECD 1982).

Recent improvements in measuring techniques and new developments in monitoring strategies have revived interest in primary production as an index to define trophic (Andersen et al. 2006) although there is still a controversy about the measurement units (Smith 2007). One alternative unit already discussed by Vollenweider (1968) is the ‘activity

Fig. 9.4 Regression of annual primary production on solar radiation modified from Jónasson et al. (1974). Statistical analysis is inserted into the graph



coefficient' defined as carbon uptake rate per algal unit measured as cell, biomass, chl-a and carbon content. Such coefficients are sensitive indicators to describe the physiological state of algal assemblages but are not suitable for the demarcation of trophic levels because their quantities usually all fall into a narrow range of values (see e.g. Dokulil et al. 2005; Fig. 9.4).

The controversy about the correct reference to define trophic boundary conditions from photosynthetic rate measurements substantiated in different entities used. According to Findenegg (1964), the vertical distribution of daily production often is a better indicator of trophic than integrated rates (Dokulil et al. 2005; Dokulil and Kaiblinger 2009). Using the data on average volumetric euphotic zone production (A) from Fig. 9.2 and the delineation proposed therein, a gradient of trophic categories can be produced from the 252 observations (Fig. 9.5).

The number of data points at each trophic level indicates a slight under-representation of hypereutrophic examples. If the two oligotrophic levels are considered as one category as well as the two eutrophic levels, their number of data points, 95 and 93 respectively, are almost the same, which indicates that both trophic groupings are equally represented in the data set. Confidence intervals (notches, Fig. 9.5) show that

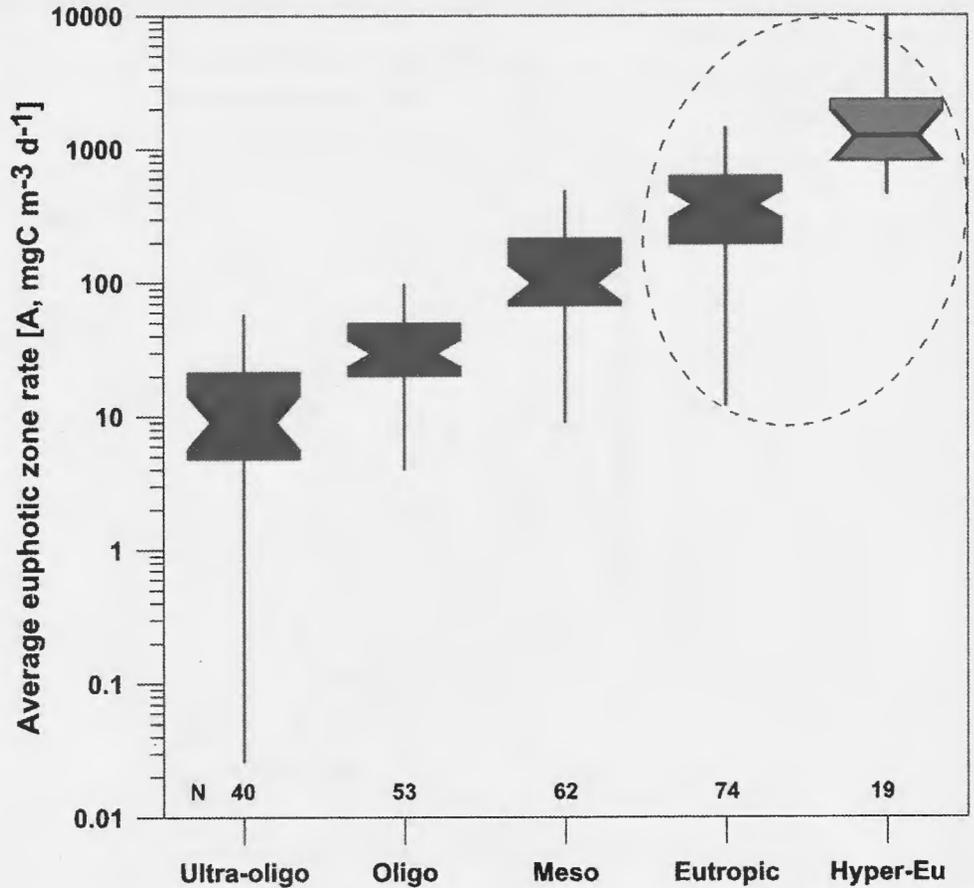
results are statistically significant because they do not overlap. The inter-quartile range (IQR) systematically increases from 16.7 at the ultra-oligotrophic level to 1,529 at the hypertrophic end demonstrating the high variability of production rates under eutrophic conditions. The minimum–maximum range of ultra-oligotrophic waters spans 3 orders while all others vary between 1 and 2 orders.

A volumetric production at optimum depth (A_{opt}) of about 200–300 mg C m⁻³ d⁻¹ has been suggested by Vollenweider (1968) as a boundary setting between oligo-mesotrophic and Eu-hypertrophic waters. Integral column production (ΣP) can be estimated from A_{opt} using modifications of a simple model developed by Talling (1957, 1970), which proved useful in many cases but underestimates under-hypertrophic conditions (Robarts 1984). For a nutrient-rich turbid tropical lake, empirical estimates were possible from a combination of A_{opt} , chl-a and euphotic depth z_{eu}

$$\Sigma P = 2.5(A_{opt} \cdot \text{Chl-a} \cdot z_{eu}) + 46.8 \quad (9.1)$$

Column production (ΣP) increasingly depends on the most productive layer (A_{opt}) the higher the trophic level is of a lake (Rodhe 1958). This observation was used to define trophic levels from the relation daily carbon uptake rate at

Fig. 9.5 Notched box whisker graphs of the average euphotic zone rates



optimum depth to daily column carbon production (Klapper 1992, p. 79)

$$\frac{A_{opt}}{\Sigma P} \frac{mgCm^{-3}d^{-1}}{mgCm^{-2}d^{-1}} (\%) \quad (9.2)$$

Oligotrophic	Mesotrophic	Eutrophic	Polytrophic	Hypertrophic
≤15	15–30	30–75	75–90	>90

A graphical approach modified from Vollenweider (1968) provides an elegant summary of the volumetric versus integrated rate controversy (Fig. 9.6).

A range of maximum and mean attenuation coefficients supply additional information on light availability, water transparency and indirectly on lake depth. As optimum carbon uptake rates at varying attenuation coefficients increase, column production tends to decline because of reduced light availability (higher attenuation coefficients) as a consequence of self-shading by enhanced algal biomass. Figure 9.6 also illustrates the potential variability of carbon uptake rates within a broad range of possible attenuation coefficients representing clear to turbid conditions. The potential range, however, is strongly reduced at high

trophic level. Some examples of individual lakes or geographical regions are inserted to demonstrate the range of carbon uptakes commonly encountered. Some examples from European alpine lakes can be found in Dokulil (2005; Fig. 9.6). Eutrophic lakes in warm regions of the world such as Egypt, East Africa and China are good examples of highly productive waters. The theoretical maximum rate, which has been derived from theoretical considerations by Vollenweider (1965a), can be described by an exponential equation

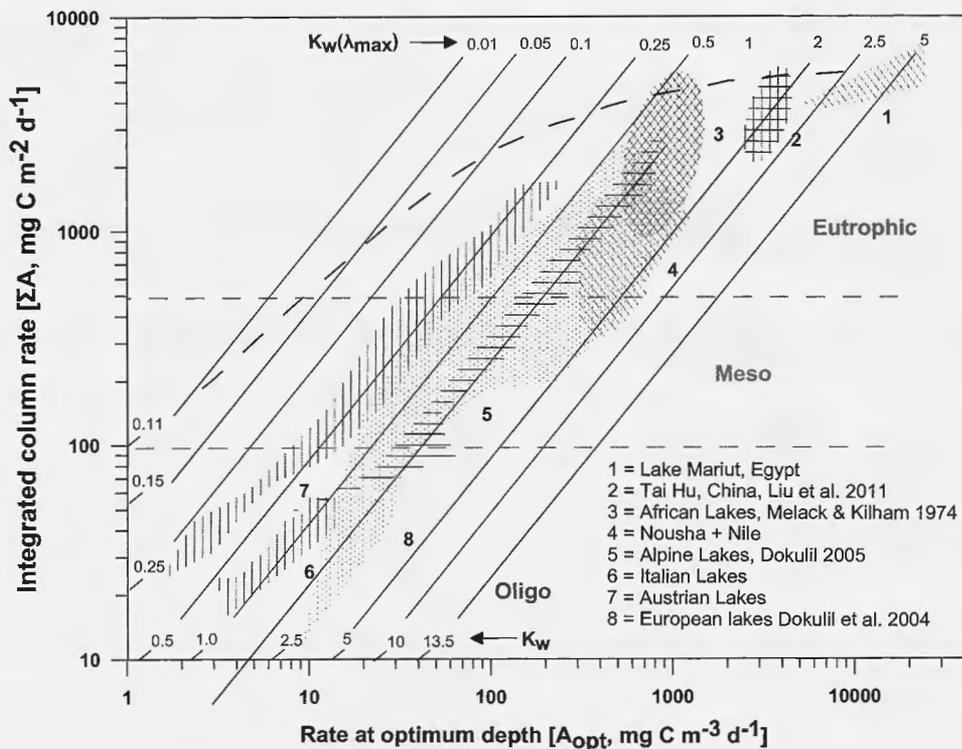
$$\Sigma P = 2952.563 \times (1 - \exp(-0.014A_{opt})) + 2595.813 \times (1 - \exp(-0.00094A_{opt})), r^2 = 0.99, p < 0.0001 \quad (9.3)$$

Based on earlier arguments and formulations, Bannister (1974) developed an equation for the upper limit of production, which is identical to the one given by Vollenweider (1968, p. 43).

$$\Sigma P [gCm^{-2}d^{-1}] = f_i \times A_{opt}/k_w \quad (9.4)$$

with $f_i=2.5$ (2–3.5)—Vollenweider (1968), $f_i=2.3$ —Bannister (1974) and k_w attenuation coefficient.

Fig. 9.6 Daily integrated column rate (ΣA) versus rate at optimum depth (A_{opt}) for different minimum attenuation coefficients (diagonal lines, $K_w(\lambda_{max})$) and total attenuation (K_w). The dashed line indicates theoretical upper limits of production (see text for further explanation). Different shadings show the area of different lake regions or specific lakes in the world. Numbers in the legend specify these lakes and are, if not otherwise stated, from Vollenweider (1968). Trophic limits inserted. Diagram modified from Vollenweider (1968)



Similarly, annual production ($\Sigma\Sigma P$) can be predicted from chl-a concentration, light attenuation coefficient (k_w) and the chl-a specific extinction coefficient (η) using an equation developed by Vollenweider (Clasen and Bernhardt 1980)

$$\Sigma\Sigma P [\text{g C m}^{-2} \text{y}^{-1}] = K \frac{\text{Chl} - a}{k_w + \eta \times \text{Chl} - a} \quad (9.5)$$

A more intensive discussion of depth-time integrated production calculation and associated models can be found in Rodhe (1965) and Vollenweider (1965a, b, 1970).

Kimmel et al. (1990) provided a detailed table of the magnitude and variability of ΣA in reservoirs of different trophic. On an annual basis, phytoplankton production is not significantly different from phytoplankton production in natural lakes (Brylinsky 1980; Wetzel 2001, p. 386 ff.). Daily productivity in most reservoirs, however, is likely more variable than in most natural lakes. About 30–40% of the lakes and reservoirs included in these references are eutrophic. This is certainly an underestimation because most of the waters worldwide are small and shallow with plenty of light and nutrients (Downing et al. 2006; Downing 2010). This group therefore should be among the most productive systems of the world (Lewis 2011). Similarly, productivity of large rivers is likely to rise owing to increasing eutrophication (Dokulil 2012). Global change will further enhance freshwater eutrophication (Dokulil and Teubner 2011).

9.5 Defining Trophic Boundary Conditions

Trophic boundaries were commonly deduced from column integrated rates per square metre of lake surface (mg m^{-2}) either per day or per year.

Boundaries defined for integral daily rates by Henderson-Sellers and Markland (1987) in Table 9.1 are not very different from those by Schönborn (2003). Trophic levels were expanded to cover hypertrophic conditions by Håkanson and Boulion (2001).

Their ranges of average annual production (Table 9.2) are much lower for the trophic categories than those stated by Schönborn 2003 (Table 9.1).

Håkanson and Boulion (2001) then further added an ultra-oligotrophic level basing trophic classification on fixed steps of mean summer chl-a using a factor of 10 (Table 9.3) which was also used earlier by Håkanson and Peters (1995; Table 9.3) in their modelling approach.

Limits by Wetzel (2001) are higher particularly for eutrophic conditions. In addition, his system expands the trophic categories by adding ultra-oligotrophic and dystrophic levels (Table 9.4)

Klapper (1992) and Felföldy (1987) considerably expanded and refined trophic categories to be able to better differentiate lakes in regions where waters are primarily at higher trophic level (Tables 9.4 and 9.5).

Table 9.1 Ranges of chlorophyll-a (chl-a), daily column production and annual production for three trophic levels

Trophic level	Chl-a ^a (mg m ⁻³)	Daily production ^a (mg C m ⁻² d ⁻¹)	Daily production ^b (mg C m ⁻² d ⁻¹)	Annual production ^b (g C m ⁻² y ⁻¹)
Oligotrophic	0–4	30–100	0–200	<100
Mesotrophic	4–10	100–300	200–500	100–150
<i>Eutrophic</i>	10–100	300–3,000	500–4,000	150–250

^aModified from Henderson-Sellers and Markland (1987, p. 200)^bModified from Schönborn (2003, p. 255)**Table 9.2** Trophic boundaries of total phosphorus (TP), chlorophyll-a (chl-a), algal fresh weight and yearly production for four trophic levels. (Modified from Håkanson and Jansson 1983)

Trophic level	Total-P (mg m ⁻³)	Chl-a (mg m ⁻³)	Algal fresh wt. (g m ⁻³)	Annual production (g C m ⁻² y ⁻¹)
Oligotrophic	<10	<2.5	<0.8	<30
Mesotrophic	8–25	2–8	0.5–1.9	25–60
<i>Eutrophic</i>	20–100	6–35	1.2–2.5	40–200
<i>Hypertrophic</i>	>80	30–400	2.1–20	130–600

Table 9.3 Trophic classification based on fixed steps (factor 10) of mean summer chlorophyll-a (chl-a) concentrations and adding an ultra-oligotrophic level. (Modified from Håkanson and Bouillon 2001)

Trophic level	Total-P (mg m ⁻³)	Chl-a (mg m ⁻³)	Daily rate (mg C m ⁻³ d ⁻¹)	Annual production (g C m ⁻² y ⁻¹)
Ultra-oligotrophic	<3	≤0.1	≤4.4	≤12.5
Oligotrophic	1–10	≤1	≤32	12.5–38
Mesotrophic	5–40	≤10	≤270	38–140
<i>Eutrophic</i>	20–400	≤100	≤2,400	140–640
<i>Hypertrophic</i>	>100	≤1,000	>2,400	>640

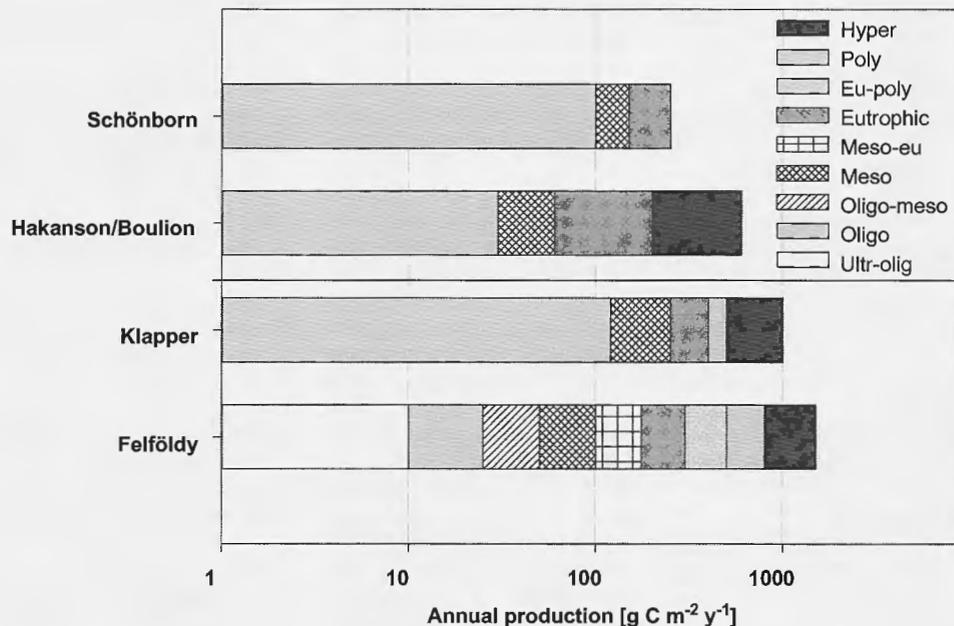
Table 9.4 Trophic classification for seven trophic categories based on chlorophyll-a (chl-a) and column production either per day or per year

Trophic level	Chl-a ^a (mg m ⁻³)	PP ^a (mg C m ⁻² d ⁻¹)	Chl-a ^b (mg m ⁻³)	PP ^b (g C m ⁻² y ⁻¹)
Ultra-oligotrophic	0.01–0.5	<50		
Oligotrophic	0.3–3	50–300	<3	<120
Mesotrophic	2–15	250–1,000	3–10	120–250
<i>Eutrophic</i>	10–500	>1,000	10–20	250–400
<i>Polytrophic</i>			20–60	400–500
<i>Hypertrophic</i>			>60	>500
Dystrophic	0.1–19	50–500		

^aModified from Wetzel (2001, p. 389)^bModified from Klapper (1992, p. 79)**Table 9.5** Trophic boundaries for chl-a, daily column production and annual production dividing the trophic continuum into nine trophic levels. (Modified from Dokulil 2003 after Felföldy 1987)

	Chlorophyll-a (mg m ⁻³)	Daily production (mg C m ⁻² d ⁻¹)	Annual production (g C m ⁻² y ⁻¹)
Ultra-oligotrophic	<1	<50	<10
Oligotrophic	1–3	50–125	10–25
Oligo-mesotrophic	3–10	125–250	25–50
Mesotrophic	10–20	250–500	50–100
Meso-eutrophic	20–50	500–900	100–175
<i>Eutrophic</i>	50–100	900–1,500	175–300
<i>Eu-polytrophic</i>	100–200	1,500–2,500	300–500
<i>Polytrophic</i>	200–800	2,500–4,000	500–800
<i>Hypertrophic</i>	>800	>4,000	>800

Fig. 9.7 Comparative graphical representation of trophic boundary conditions from four authors using data for annual average column production from Tables 9.1, 9.2, 9.3 and 9.4. Note logarithmic x-axis



Both systems have similar boundaries at both average daily and annual rates. The annual boundaries proposed by these authors are compared in Fig. 9.7.

9.6 Global Production

In a recent analysis on global primary production of lakes, Lewis (2011) concluded that maximum rates of photosynthesis centre at about $10 \text{ g C m}^{-2} \text{ d}^{-1}$, equivalent to $3,650 \text{ g C m}^{-2} \text{ y}^{-1}$. Earlier estimates range from $8\text{--}13 \text{ g C m}^{-2} \text{ d}^{-1}$ (Melack and Kilham 1974; Uhlmann 1978; Talling 1982; Talling and Lemoalle 1998).

According to Pace and Prairie (2005), global gross primary production (GPP) of lakes is about 0.65 Pg C y^{-1} , which might be an underestimate since it does not emphasize the high production of small lakes, which are estimated to dominate globally (Downing et al. 2006). Within the global GPP of $100\text{--}150 \text{ Pg C y}^{-1}$ (Randerson et al. 2002) global internal primary production of lakes represents only a minor fraction of global primary production.

Understanding global limnology and global photoautotrophic production of lakes, ponds, rivers, streams and wetlands becomes increasingly important in a warmer world (Dokulil 2009; Dokulil and Teubner 2011). We need to quantify and understand the role of continental waters within the biosphere as water becomes a limited resource. The population of the world needs aquatic services and intact inland aquatic systems for sustainable life.

9.7 Conclusions

Climatic changes anticipated for the near future will certainly strongly affect inland waters globally both qualitatively and quantitatively (e.g. Burroughs 2001). One of the most severe impacts is eutrophication impairing water quality (Ansari et al. 2011; Dokulil and Teubner 2011). Changes in trophic level will also affect classification of lakes within the Water Framework Directive (Frisk and George 2010). Trophic boundaries and reference conditions need to be adapted to accommodate these pressures. Multidisciplinary approaches are needed to maintain water supply and solve socioeconomic consequences (Bateman and Georgiou 2010; Janus 2010). Management of water resources must include long-term monitoring strategies and model development. In this context, interest in primary production measurements as the best index of trophy must be reconsidered particularly since new fluorescence techniques allow continuous recording of relevant parameters.

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