

Research Article

Effects of alpine hydropower operations on primary production in a downstream lake

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Abstract. During the past century, the construction of hydropower dams in the watershed of Lake Brienz has significantly altered the dynamics of turbidity, which has important implications for lake productivity. To assess these effects, we measured *in situ* carbon assimilation rates and ambient light intensities over 18 months. Based on experimental data, a numerical model was developed to assess gross primary production under present light conditions and those under a hypothetical case without upstream dams. Light conditions for the hypothetical ‘no-dam’ situation were estimated from pre-dam Secchi depths and simulated ‘no-dam’ particle concentrations.

Current gross primary production is low ($\sim 66 \text{ gC m}^{-2} \text{ yr}^{-1}$), and could increase $\sim 44\%$ if the lake was less turbid. Disregarding nutrient retention in reservoirs, we estimate gross primary production would be $\sim 35\%$ lower in summer and $\sim 23\%$ higher in winter in the absence of reservoirs. The annual primary production ($\sim 58 \text{ gC m}^{-2} \text{ yr}^{-1}$) would decrease $\sim 12\%$ compared to the current primary production with dams. According to model calculations, hydropower operations have significantly altered the seasonal dynamics, but have little effect on annual primary production in Lake Brienz.

Key words. Dams and reservoirs; downstream effects; turbid lakes; light regime; oligotrophic lakes.

Introduction

Lacustrine ecosystems are strongly influenced by catchment characteristics (Duarte and Kalff, 1989; Kratz et al., 1997; Dixit et al., 2000). In particular, the construction of 500,000 reservoirs during the second half of the 20th century has altered the hydrology of downstream rivers and lakes (McCully, 1996; Vörös-

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Table 1. Characteristics of Lake Brienz and Lake Thun.

Property	Unit	Lake Brienz	Lake Thun	Reference
Surface area	km ²	29.8	48.4	(Finger et al., 2006)
Volume	km ³	5.17	6.44	(Finger et al., 2006)
Maximum depth	m	259	217	
Average depth	m	173	135	
Altitude of lake level	m asl	564	558	(LHG-BWG, 2005)
Average discharge at outflow in 2004 ⁽¹⁾	m ³ s ⁻¹	59.7	108	(LHG-BWG, 2005)
Average residence time	yr	2.7	1.9	
Average water temperature ⁽²⁾	°C	9.5	10.9	
Average euphotic depth ⁽³⁾	m	15.2	21.7	

⁽¹⁾ Data publicly available at: <http://www.bwg.admin.ch/service/hydrolog/d/>

⁽²⁾ Average water temperature in the top 10 m of the lake based on monthly CTD-profiles between 1999 and 2005.

⁽³⁾ Average euphotic depth based on monthly PAR-profiles between 1999 and 2005.

marty et al., 1997; Vörösmarty et al., 2003). The ecological and social effects of water storage on downstream regions have been well studied (Rosenberg et al., 1995; Rosenberg et al., 1997; Rosenberg et al., 2000), especially with regard to the biological impacts on rivers (Ward and Stanford, 1995; Nilsson et al., 1997; Hart and Poff, 2002) and occasionally on downstream lakes (Ashley et al., 1997; Stockner et al., 2000; Friedl and Wüest, 2002). In terms of glaciated catchments, reservoirs retain much of the glacial till (Anselmetti et al., 2007) and thus alter the allochthonous particle input to downstream lakes, which in turn affects the dynamics of turbidity (Finger et al., 2006) and nutrient inputs (Humborg et al., 2000; Friedl et al., 2004). Moreover, suspended particles can significantly reduce light penetration, and thus limit primary production (Jewson and Taylor, 1978; Krause-Jensen and Sand-Jensen, 1998) and reduce the visual range of aquatic animals (Aksnes and Utne, 1997).

The general relation between light intensity (photosynthetically active radiation; PAR) and photosynthesis, measured using the ¹⁴C method (Stemann Nielsen, 1952), provides the basis for modelling the primary production of a water body as a function of light availability (Jassby and Platt, 1976; Platt and Jassby, 1976; Platt et al., 1980). In simple cases, such models can be used to estimate primary production under varying light conditions (Sakshaug and Slagstad, 1991), neglecting the effects of internal mixing (Diehl, 2002), sediment resuspension (Schallenberg and Burns, 2004), plankton competition for nutrients (Litchman et al., 2004), or changes in nutrient availability (Müller et al., 2007a).

Lake Brienz, situated at the foothills of the Alps in the *Bernese Oberland*, Switzerland, provides an ideal system to study the effects of turbidity on primary production. Over 20% of the catchment is covered by glaciers, leading to the highest particle input per catchment area (324 t km⁻² yr⁻¹) in Swiss lowland lakes (Finger, 2006). As a result, Lake Brienz becomes turbid during summer when snow

and glacier melting reaches a maximum. The construction of several hydropower facilities in its catchment has significantly altered the hydrological regime and particle inputs.

The purpose of this study is to assess the effects of altered turbidity regimes on the primary productivity of Lake Brienz using monthly profiles of *in situ* carbon (C) assimilation rates and numerical relationships between *in situ* primary production and *in situ* light intensity. These data were used to develop a mathematical model to estimate carbon assimilation rates between 1999 and 2005. To evaluate the effects of suspended particles, this calibrated model was used to estimate primary production in neighbouring Lake Thun, which is almost identical in an eco-geographical sense, but practically free of inorganic turbidity. Finally, the model is used to explore conditions prior to dam construction and to quantify the effects of hydropower dams on primary production in Lake Brienz.

Lake Brienz

Lake Brienz is situated about 70 km southeast of Bern (7° 58' E, 46° 43' N), with a surface area of 29.8 km², volume of 5.17 km³, and maximum depth of 259 m, which is typical of peri-alpine lakes in Switzerland (Table 1). Two major inflows, the Aare and Lütschine, enter the lake at opposite ends (Fig. 1). These two tributaries drain a catchment area of 933 km² and carry average particle concentrations of ~160 g m⁻³, resulting in an annual suspended particle input of ~300 kt yr⁻¹ (Finger et al., 2006). Over half of this mass enters into the surface layer, leading to average particle concentrations in the top 50 m of the lake of up to 25 g m⁻³ (Finger et al., 2006). Only about 9 kt yr⁻¹ (or 3%) of the particles are discharged downstream into Lake Thun (Fig. 1).

Unlike the Lütschine, whose hydrological regime has remained mostly natural, the Aare is character-

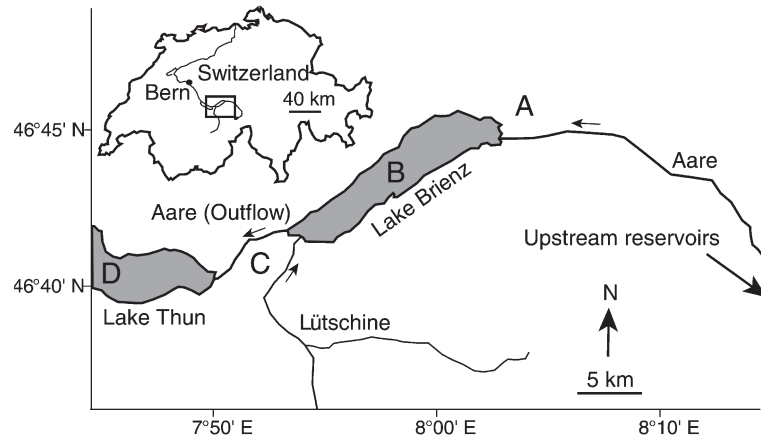


Figure 1. Overview of the study area including the sampling sites within and around Lake Brienz. Site A (only surface), B and D depict locations of photosynthetically active radiation (PAR) measurements. Site B marks the lake water sampling position. Site C localizes the continuous global radiation monitoring site operated by MeteoSwiss. Small arrows show river flow directions. Hydropower reservoirs are situated 15 km upstream on Aare (large arrow indicates direction).

Table 2. Overview of sampling program.

Parameters	Symbol	Location ⁽¹⁾	Sampling period	Unit	Frequency of sampling	Performed by
¹⁴ C Assimilation ^(2,3)	P^B	B	2004/5	mgC m ⁻³ h ⁻¹	monthly	authors
Chlorophyll a ^(2,3)	$Chla$	B	2004/5	mg m ⁻³	monthly	authors
Chlorophyll a ⁽⁴⁾	$Chla_{mean}$	B	1999–2005	mg m ⁻³	monthly	GBL
<i>In situ</i> PAR ^(3,5)	$I_{in-situ}$	B	1999–2005	μE m ⁻² s ⁻¹	monthly	authors/GBL ⁽⁵⁾
<i>In situ</i> PAR (Lake Thun)	$I_{in-situ}$	D	1999–2005	μE m ⁻² s ⁻¹	monthly	GBL
PAR at surface ⁽³⁾	I_s	A	2004/5	μE m ⁻² s ⁻¹	monthly	authors
Global radiation	$I_s^{MeteoSwiss}$	C	1999–2005	W m ⁻²	hourly	MeteoSwiss
CTD ⁽⁶⁾	T; Tr	B	1999–2005	°C; %	monthly	GBL/authors
CTD (Lake Thun)	T	D	1999–2005	°C	monthly	GBL
Secchi depth ⁽⁷⁾	s_d	B	1921–1922 1993–2005	m	varying	diverse
Reactive phosphorus	SRP	B	2003–2004	mgP m ⁻³	~monthly	authors

⁽¹⁾ Locations marked in Figure 1.

⁽²⁾ Chlorophyll a and ¹⁴C assimilations were determined at the following depths (m): 0, 0.5, 1, 1.5, 2.5, 3.75, 5, 7.5, 10, 12.5, 15, 20, 25, 30, and 35 (note: before 30 March 2004 samples were only collected to a depth of 25 m).

⁽³⁾ Sampling dates: 18 December 2003; in 2004: 3 March, 30 March, 4 May, 8 June, 6 July, 27 July, 25 August, 21 September, 20 October, 23 November, 15 December; in 2005: 9 March, 5 April, and 3 May.

⁽⁴⁾ Chlorophyll a determined by GBL on a monthly basis for integrated water samples (0 to 20 m depth).

⁽⁵⁾ *In situ* PAR-profiling has been conducted by GBL on a monthly basis since 1999 and by the authors during each P^B -sampling.

⁽⁶⁾ CTD profiling comprises temperature, conductivity and light transmission (Tr: percentage of light transmitted over a path length of 0.1 m). CTD profiling is conducted since 1997 by GBL in the framework of a regional monitoring; additional CTD profiling was conducted during P^B -sampling.

⁽⁷⁾ Secchi recordings are conducted by GBL since 1993; historic data from 1921 and 1922 were collected by Flück (1926). Since 1993 recordings exist twice a week; before 1993 recording resolution is varying.

ized by a complex damming system, operated by the *Kraftwerke Oberhasli AG*. Over 60% of the annual discharge in the Aare is stored in reservoirs and released when electricity demand is high. According to seismic measurements, ~232 kt yr⁻¹ of sediments are retained annually in these hydropower reservoirs (Anselmetti et al., 2007), indicating that the particle load to Lake Brienz has been reduced by 45% since 1932 (Finger et al., 2006). Moreover, the operation of the hydropower reservoirs has decreased turbidity in Lake Brienz in the summer through particle retention, and increased turbidity during winter through hydro-

power production (Finger et al., 2006). Based on these findings, Jaun et al. (2007) concluded that the altered particle dynamics led to a doubling of light attenuation during winter and a reduction of ~50% during summer.

In addition to the aforementioned changes in hydrology and particle input, there have been some recent changes noted in the biology of the lake. Specifically, time series of phytoplankton and zooplankton indicate a continuous decline in biological activity in the lake since 1994 (Rellstab et al., 2007). Investigations of whitefish growth rates indicate that

the whitefish (*Coregonus fatioides*), feeding mainly on *Daphnia* (Cladocera), were undernourished (Müller et al., 2007b). Moreover, there was a drastic collapse (> 90%) in the fishing yield in 1999, which coincided with the quasi-disappearance of *Daphnia* (primarily *Daphnia hyalina*) (Wüest et al., 2007). These observations suggest that the loss of *Daphnia* was due to reduced algal production through bottom-up control, which may have been caused by: (1) a decrease of particulate and dissolved bio-available phosphorus (bio-P) as a consequence of sewage treatment and trapping of nutrients in upstream reservoirs (Müller et al., 2007a); or (2) the reduction of *in situ* irradiance due to changes in turbidity dynamics caused by hydropower activities. Whereas the first hypothesis was evaluated in Müller et al. (2007a), here we focus on the latter hypothesis – namely the effect of turbidity on primary production.

Material and methods

Lake in situ primary production measurements

Water was sampled from 0 to 35 m depth in the centre of Lake Brienz (location B; Fig. 1) on 15 occasions between 18 December 2003 and 3 May 2005. Each sample was subdivided to determine C assimilation rates P^B ($\text{mgC m}^{-3} \text{h}^{-1}$) with the ^{14}C technique (Steemann Nielsen, 1952) and chlorophyll *a* concentration *Chla* (mg m^{-3}). Two 120 ml sub-samples were inoculated with 15 $\mu\text{Ci NaH}^{14}\text{CO}_3$ in Duran bottles (one dark sample and one with transmission properties of 22% absorption at 325 nm and 4% at 350 nm) and incubated at their corresponding depths for 4 h between 10:00 and 14:00 local time (CET). After incubation, all samples were processed by the acidic bubbling method, according to Gächter and Mares (1979). Seven ml of each sample were blended with 10 ml of InstagelTM (Packard, USA). Subsequently, the radioactivity of the sample was measured with a liquid scintillation spectrometer (TRICARB, Packard, USA) at room temperature. P^B was determined by comparing the activity in the scintillation vial before and after acid bubbling and expressed as a % fraction of added radioactive C assimilated by algal cells during incubation. The fractional amount of ^{14}C taken up by the algae multiplied by the total dissolved inorganic carbon (DIC) in the incubated water sample corresponds to the instantaneous P^B . DIC was determined from alkalinity and pH following Rodhe (1958). All P^B values were corrected for non-photosynthetic C uptake, as determined in the dark sample.

Chla was determined in each sub-sample according to DEV (1972–1989). After filtering through What-

man GF/F filters, samples were placed into Sovirel tubes filled with 8 ml 90% ethanol. Chlorophyll was extracted by heating the samples for 10 min in a water bath at 75°C and subsequent sonification (for 5 min) at room temperature. Afterwards, the *Chla* extracts were filtered through Millipore Millex FG 0.2 μm membrane filters. The *Chla* content was determined by 2 independent procedures: (a) spectrophotometrically following DEV (1972–1989) using a U2000 dual path spectrophotometer (Hitachi, Japan), and (b) with high performance liquid chromatography (HPLC). HPLC-analysis was performed according to Meyns et al. (1994) and Murray et al. (1986) by separating *Chla* isocratically at a flux rate of 1.0 ml min^{-1} in a mixture of 49.5% methanol, 45% ethyl acetate and 5.5% water. Throughout this study photometrically determined *Chla* values are presented, while the results of the HPLC analysis were used to verify the photometric results.

Additional water samples for soluble reactive phosphorus (SRP) were collected from 19 February 2003 to 7 July 2004 at various depths in the center of the lake. Samples were filtered through cellulose acetate membrane filters and SRP was determined photometrically with the ammonium molybdate method (DEV, 1972–1989).

In situ photosynthetically active radiation (PAR denoted as $I_{in-situ}$ ($\mu\text{E m}^{-2} \text{s}^{-1}$)) was measured with a scalar quantum sensor (LI 190 SB) connected to an integrating quantum meter (LI 188; LI-COR Inc, USA). A cosine corrected PAR sensor (LI 190) served as a reference, measuring PAR above the water surface (I_s) at location A (Fig. 1).

Monthly CTD profiles of conductivity, temperature, pH, light transmission and dissolved oxygen (SBE 19; Seabird USA) and PAR profiles (with a spherical underwater sensor from LI-COR Inc.) at locations B (Lake Brienz) and D (Lake Thun) have been taken by the Laboratory for Water and Soil Protection of the Canton Bern (GBL) since 1999. In addition, samples integrating from 0 to 20 m depth were collected monthly with a Schröder (1969) bottle, and analyzed for phytoplankton (including *Cyanophyceae* and *Bacillariophyceae*) and $Chla_{mean}$ (mg m^{-2}). Zooplankton was sampled with a 95- μm mesh size net (Rellstab et al., 2007).

Model approach

The specific C assimilation rate P^B per unit *Chla*, i.e. the ratio $P^{chla} = P^B / Chla$ ($\text{mgC h}^{-1} (\text{mgChla})^{-1}$), was determined for all samples to interpolate P^B in time and space between sampling dates. All P^{chla} were normalized to a reference temperature ($T_{norm} = 10^\circ\text{C}$), assuming exponential temperature-dependent growth rates:

$$P_{norm}^{chla} = P^{chla} e^{(\ln(Q_{10})[(T_{norm}-T)]/10)} \quad (1)$$

where $Q_{10} = 2$ denotes the typical factor of logarithmic growth rate increase for 10°C warming, as determined experimentally in natural waters (Eppley and Sloan, 1966; Williams and Murdoch, 1966; Eppley, 1972). Accordingly, P_{norm}^{chla} (mgC h⁻¹ (mgChla)⁻¹) denotes the C assimilation rate at T_{norm} . The value of Q_{10} in the studies cited above varies between 1.88 and 2.5, but in our case model results are not sensitive to such changes in Q_{10} (see discussion).

This temperature- and *Chla*-normalized C assimilation rate (P_{norm}^{chla}) is primarily a function of ambient light intensity ($I_{in-situ}$). We used the mathematical approach proposed by Platt et al. (1980) to interpolate P_{norm}^{chla} vertically between measured samples:

$$P_{norm}^{chla}(z) = P_S^B \left(1 - e^{-([\alpha \cdot I_{in-situ}]/P_S^B)} \right) \cdot e^{-([\beta \cdot I_{in-situ}]/P_S^B)} \quad (2)$$

where P_S^B denotes the hypothetical maximum photosynthetic output without photoinhibition; i.e., the decline in photosynthesis due to strong light fields (Powles, 1984). The empirical coefficient α denotes the increase of P_{norm}^{chla} with increasing $I_{in-situ}$ and β accounts for the decrease of P_{norm}^{chla} caused by photoinhibition. The 3 empirical coefficients (P_S^B , α and β) were determined through a least-squares fit of equation (2) to the measured P_{norm}^{chla} (Fig. 2a) and cross checked for plausibility for each sampling profile. SRP levels (Fig. 2b) limit P_S^B and were considered implicitly in the fits. Whereas convective mixing and low productivity leads to slightly higher SRP in winter, stratification and high productivity induces SRP depletion in summer. Accordingly, P_S^B varies between ~5 mgC h⁻¹ (mgChla)⁻¹ in winter and 1.6 mgC h⁻¹ (mgChla)⁻¹ in summer (Fig. 2a). As SRP values above 2 mg m⁻³ are rapidly depleted in summer, elevated SRP values can usually be attributed to recent river intrusions. Therefore, monthly sampling adequately describes seasonal evolution in SRP limitation. The light limitation factor α ranged between 0.04 and 0.25 (mgC m² s (h μE mgChla)⁻¹), and the photoinhibition factor β varied between 0.002 to 0.03 (same units as α).

In order to interpolate depth-dependent $P_{norm}^{chla}(z)$ between profiles with high temporal resolution throughout the sampling period, ambient light $I_{in-situ}(z, t)$ for the photic layer was used. We defined the *in-situ* relative light $I_{rel}(z)$ by the quotient of $I_{rel}(z) = I_{in-situ}(z)/I_s$. As $I_{rel}(z)$ is governed by suspended and dissolved substances in the water and hence not subject to short-term variation, we obtained time series of $I_{rel}(z, t)$ by linear interpolation between monthly profiles. Assuming that $I_s(t)$ is linearly

proportional to the global radiation of $I_s^{MeteoSwiss}(t)$ (W m⁻²) recorded at the MeteoSwiss monitoring site C (Fig. 1), we determined $I_{in-situ}(z, t)$ with 1-hour resolution according to:

$$I_{in-situ}(z, t) = I_{rel}(z, t) \cdot I_s(t) = I_{rel}(z, t) \cdot c \cdot I_s^{MeteoSwiss}(t) \quad (3)$$

where $c = \frac{\bar{I}_s}{I_s^{MeteoSwiss}}$ and \bar{I}_s denotes the average reference PAR (μE m⁻² s⁻¹) measured with our sensor (at location A). The empirical coefficient $c = 1.54 \mu\text{E s}^{-1} \text{W}^{-1}$ accounts for the conversion of units and different sunlight exposures of the two sites due to shadowing from the high mountains surrounding Lake Brienz.

The time series of gross primary productivity in Lake Brienz can then be estimated by linearly interpolating the coefficients P_S^B , α and β in equation (2). The back transformation of $P_{norm}^{chla}(z, t)$ from T_{norm} to ambient water temperature ($T(z, t)$) is given by:

$$P^{chla}(z, t) = P_{norm}^{chla}(z, t) \cdot e^{(\ln(Q_{10}) \cdot [(T(z, t) - T_{norm})]/10)} \quad (4)$$

By multiplying $P^{chla}(z, t)$ with instant *Chla*(z, t) – also obtained by linear interpolation – the actual $P^B(z, t)$ can be determined. Using this approach, $P^B(z, t)$ profiles are obtained with hourly resolution. The corresponding areal primary production is obtained by vertically integrating the $P^B(z, t)$ profile.

For periods beyond P^B sampling, only temperature, light attenuation and global radiation (data: MeteoSwiss) are known. Extrapolations were made by assuming α , β , P_S^B and *Chla*(z, t) as determined in 2004. Nevertheless, algal standing crop and bio-P input vary and can significantly affect P^B . In order to evaluate the potential effects of these parameters on the model results and to be able to judge the reliability of the estimated effects of turbidity, the following additional model calculations were performed:

To account for varying algae standing crops, a model run was performed in which we predicted *in situ* *Chla*(z, t) for 1999 to 2005 by assuming a proportional relation between *in situ* *Chla*(z, t) and areal $Chla_{mean}$ determined monthly by GBL:

$$Chla(z, t_y) = \frac{Chla_{mean}(t_y)}{Chla_{2004,mean}(t_y)} Chla_{2004}(z, t_y) \quad (5)$$

where t_y denotes the time elapsed in the specific year, and $Chla_{mean}(t_y)$ and $Chla_{2004,mean}(t_y)$ stand for the vertically integrated *Chla* concentrations (values between sampling: linearly interpolated). We justify

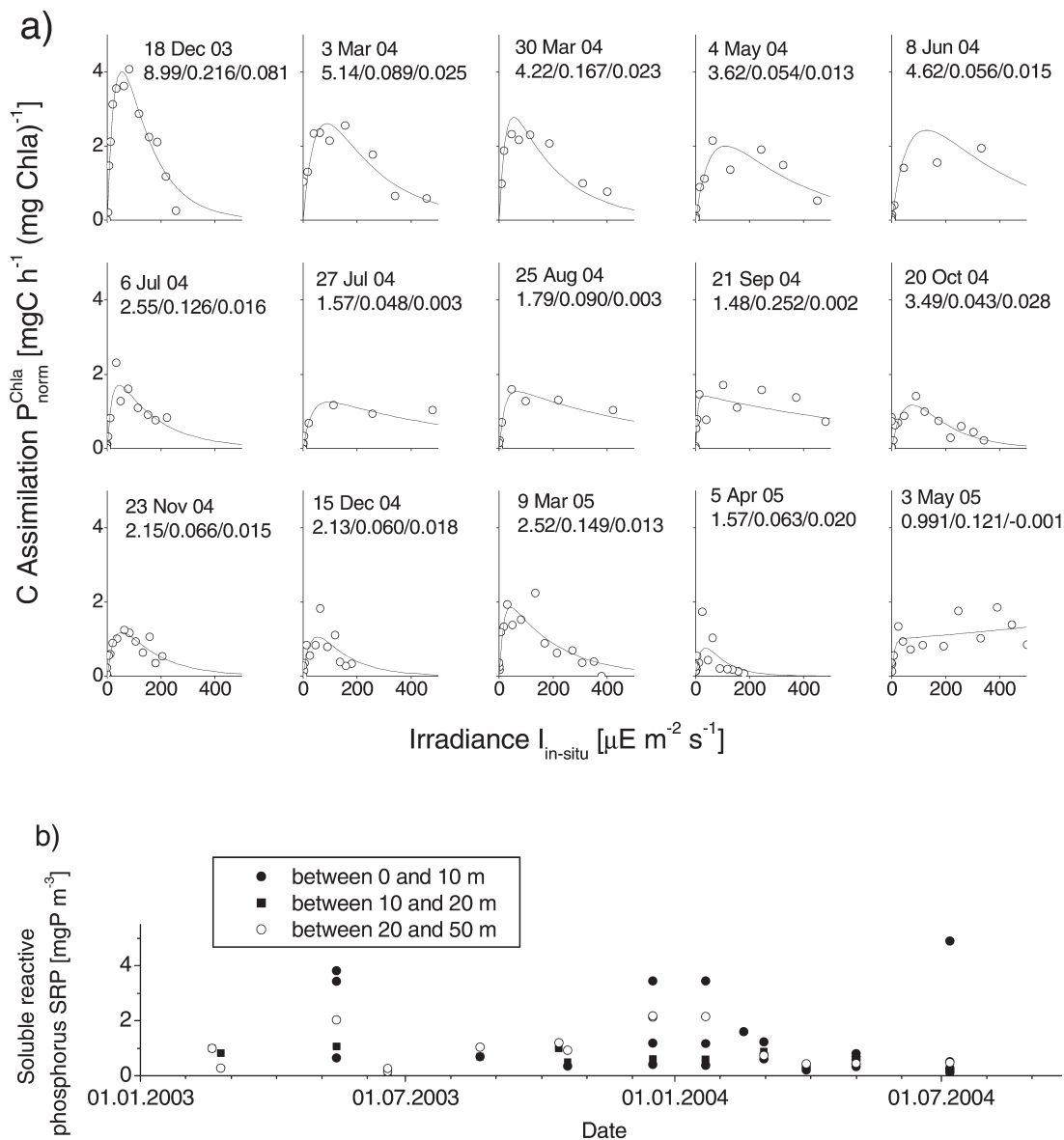


Figure 2. a) Fits of equation (2) to monthly measured *in situ* carbon assimilation profiles between 18 December 2003 and 3 May 2005. Numbers on graphs indicate date of sampling and the 3 fit values ($P_S^B/a/\beta$). b) SRP concentrations from 3 depth ranges from 19 February 2003 to 7 July 2004.

this approach by the fairly good correlation ($R^2 = 0.56$) between phytoplankton (wet biomass) and $Chla_{mean}$.

To estimate the effect of the varying bio-P input, we assumed P_S^B is linearly proportional to bio-P input of the specified year:

$$P_{S, norm}^B = \frac{P_{year}}{P_{2004}} P_S^B \quad (6)$$

where $P_{2004} = 7.8 \text{ t yr}^{-1}$ denotes the bio-P input during 2004 according to (Müller et al., 2007a) and P_{year} stands for the annual bio-P input as estimated by

Finger (2006). We justify the simple approach of equation (6) because of strong bio-P limitation.

Finally, the simulated results were compared to those from a biogeochemical model, presented in detail by Finger (2006), which considers phosphorus cycling, phytoplankton, zooplankton, physical mixing processes, nutrient loadings, water discharge and turbidity.

Estimation of primary production in clear water

The drastic collapse in fishing yield after the flood of 1999 was limited to Lake Brienz, whereas the fishery in downstream lakes (affected also by flooding but not turbidity; e.g. Lake Thun, Lake Biel) was not affected.

Hence, we compared the modelled primary production in Lake Brienz with those of turbidity-free Lake Thun. We used equations (1) to (4) for Lake Brienz as well as temperature and *in situ* light data from Lake Thun (location D; Fig. 1) to calculate the hypothetical P^B rates from 1999 to 2005 in turbidity-free water. As these simulations rely on the algorithm calibrated for Lake Brienz, the results provide only a relative comparison for the effects of turbidity.

Estimation of primary production under pre-dam conditions

To assess the effects of hydropower damming, we estimated primary production for the hypothetical situation with light conditions as in the 1920s (pre-dam) but with nutrient conditions similar to today (Müller et al., 2007a). We used recorded Secchi depths (s_d) from Flück (1926) to reconstruct ‘no-dam’ light conditions. Light attenuation coefficients (K_0) and s_d can be correlated according to Jaun et al. (2007):

$$K_0 = \frac{\ln(I_{z_0}/I_{z_{eu}})}{z_{eu} - z_0} = k_1 + \frac{k_2}{s_d} \quad (7)$$

where z_0 and z_{eu} correspond to the surface level (water-side) and euphotic depths, respectively. The right side of equation (7) describes the empirical relation between measured K_0 and s_d . Jaun et al. (2007) determined $k_1 = 0.22 \text{ m}^{-1}$ and $k_2 = 0.69$ for intense turbidity periods (May to September) and $k_1 = 0.11 \text{ m}^{-1}$ and $k_2 = 0.61$ for reduced turbidity periods (October to April). For a given K_0 , the corresponding light profile in the lake for the instant global radiation is given by:

$$I_{in-situ}(z) = I_s e^{-K_0 z} \quad (8)$$

In order to estimate $P^B(z, t)$ for light conditions in 1921 and 1922, we used the light attenuation determined from equations (7) and (8) and the fits of equation (2) during 2004. Given K_0 , the euphotic depth z_{eu} ($= \ln(100)/K_0$) is calculated as the depth where *in situ* light reaches 1% of surface light (Kirk, 1994). As the Secchi recordings in 1921 and 1922 may not represent typical pre-dam conditions, a model calculation for an average ‘no-dam’ scenario was also undertaken. For this purpose, simulated suspended particle concentrations for a hypothetical ‘no-dam’ situation (i.e., without any hydropower operation affecting the hydrological input to Lake Brienz) were adopted from Finger et al. (2006). K_0 for this ‘no-dam’ scenario was determined according to the following regression:

$$K_0 = k_3 + k_4 \cdot PC \quad (9)$$

with $k_3 = 0.06 \text{ m}^{-1}$ and $k_4 = 0.26 \text{ m}^2 \text{ g}^{-1}$ during periods of intense surface turbidity, $k_3 = 0.08 \text{ m}^{-1}$ and $k_4 = 0.08 \text{ m}^2 \text{ g}^{-1}$ during periods of reduced surface turbidity and PC (g m^{-3}) denoting suspended particle concentration in the upper 50 m of the water column in Lake Brienz (Jaun et al., 2007). Hence, primary production under typical ‘no-dam’ light conditions was estimated using predicted K_0 (equation 9) and the fits of equation (2) during 2004.

Results

Boundary conditions for primary production during sampling period

The dynamics of the 5 parameters that affect primary production in Lake Brienz (SRP, T , $I_s^{MeteoSwiss}(t)$, $I_{rel}(z)$ and *Chla*) are evaluated below. The SRP concentration was low both in the lake (usually $< 1 \text{ mg m}^{-3}$) and in the Aare and Lütschine tributaries (Müller et al., 2007a). SRP was depleted by algae as soon as it entered the lake in summer, whereas in winter SRP reached slightly higher levels due to deep convective mixing (Fig. 2b). This seasonal pattern has to be considered with caution, as SRP levels (i) vary with discharge and (ii) are close to the detection limit.

The time-averaged temperature in both inflows of Lake Brienz lies at $\sim 5.9^\circ\text{C}$ due to glaciers ($\sim 20\%$ of the catchment) (Finger et al., 2006). Thus the surface temperature in Lake Brienz rarely exceeded 20°C (Fig. 3a). Although global radiation during winter was somewhat limited by the high mountains to the south of the lake, the mean sunshine duration of 1929 h yr^{-1} (1997 to 2004; location C) was slightly above the typical Swiss average (1600 to 1900 h yr^{-1}). The rather harsh winters led to convective mixing, which frequently reached the maximum depth of the lake.

The allochthonous inorganic particle input of $> 300 \text{ kt yr}^{-1}$ (Finger et al., 2006) led to a mean light attenuation of ~ 0.5 to $\sim 0.6 \text{ m}^{-1}$ during the summer (Jaun et al., 2007). Consequently, *in situ* relative light (I_{rel}) was governed primarily by suspended particle concentrations, as illustrated in Figure 3b. Thus, the euphotic depth reached 27 m in early spring, whereas during summer, when particle concentrations were highest, the euphotic depth dropped to $< 7 \text{ m}$. Secchi depths were $> 7 \text{ m}$ deep during winter and $< 2 \text{ m}$ during summer.

The *in situ* light conditions appeared to govern the distribution of *Chla*, phytoplankton and zooplankton (Fig. 4a). During winter, plankton and *Chla* were at a seasonal minimum, mainly due to short day length ($\sim 5 \text{ h}$) and deep convective mixing. In spring when light penetration was elevated, increased *Chla* of $\sim 1.5 \text{ mg m}^{-3}$ was observed between 0 and 20 m depth.

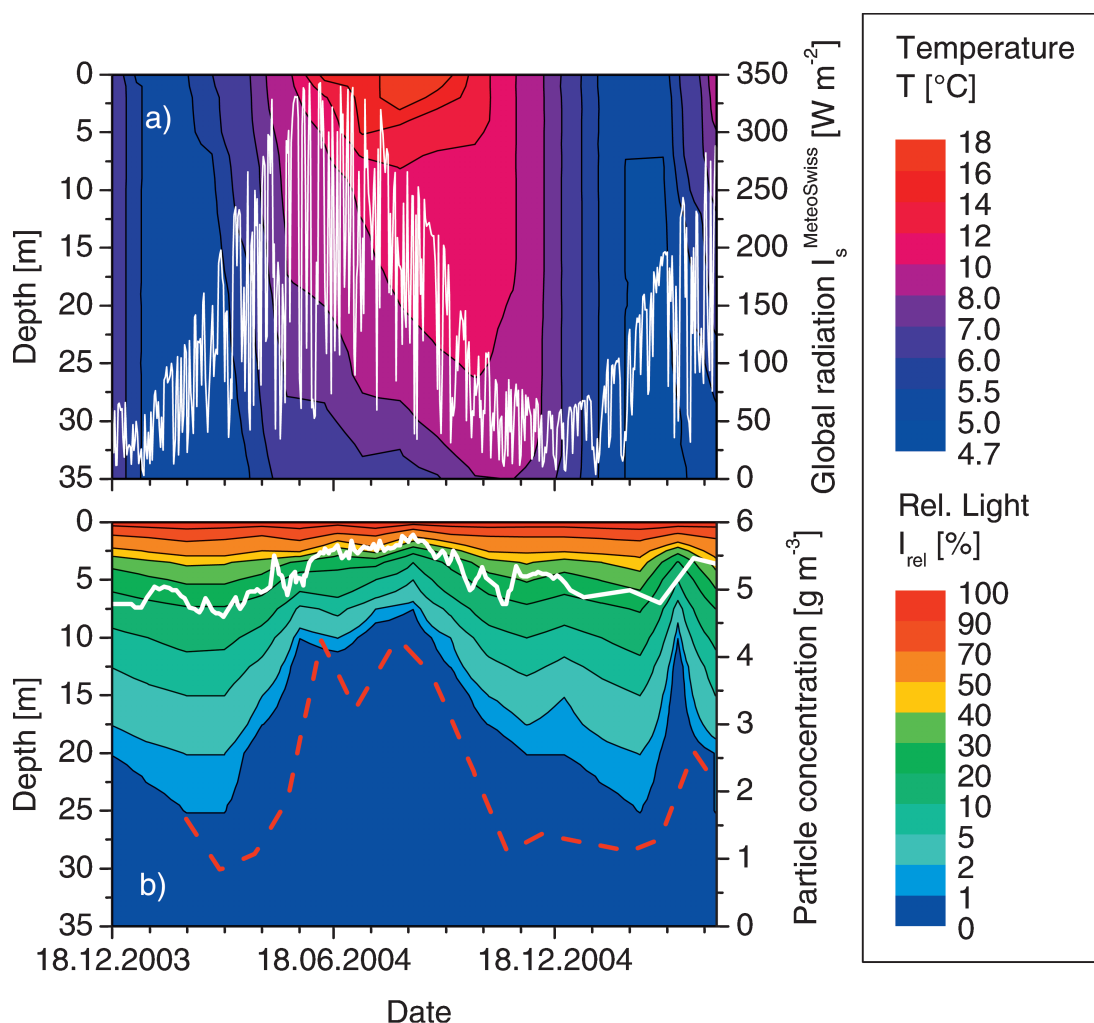


Figure 3. Physical conditions from 18 December 2003 to 3 May 2005 in Lake Brienz: a) *In situ* water temperature (contour plot) and mean daily global radiation (solid line; right scale). b) *In situ* PAR relative to surface PAR ($I_{rel} = I_{in-situ} / I_s$; contour plot). The solid white line represents Secchi depth recordings (left scale) and the red dashed line illustrates average particle concentration (right scale) in the uppermost 50 m, determined with monthly light transmission profiles according to Finger et al. (2006).

On 8 June 2004, a maximum of 4.8 mg m^{-3} was reached at 12.5 m depth (confirmed by HPLC). Since measured P^B was enhanced as well, the sample did not create artefacts in model calculations. This high value of *Chla* may be explained by short-term dynamics in plankton biomass (algae spring bloom and subsequent grazing by zooplankton), which cannot be resolved in profiles at monthly intervals (Finger, 2006). During the turbid summer, *Chla* reached values above 2 mg m^{-3} at ~3 m depth, whereas below 10 m depth *Chla* did not exceed 0.25 mg m^{-3} . Zooplankton concentrations reached their maximum in June, just after the spring algal bloom.

Primary production during the sampling period

The seasonal evolution of productivity can be described in four phases:

(1) Winter (December – March): in the winter phase deep convective mixing occurred (Finger et al., 2006) and day length was reduced ($\sim 5 \text{ h d}^{-1}$). Consequently, algae were continuously mixed beneath the euphotic depth, limiting algae biomass in the top 20 m to 3 g m^{-2} (Fig. 4a). Although euphotic depth reached up to 27 m, productivity remained at a minimum with an average *in situ* areal primary production of $78 \text{ mgC m}^{-2} \text{ d}^{-1}$ (Fig. 4b). Even at the surface, primary production was usually below $10 \text{ mgC m}^{-3} \text{ d}^{-1}$, but nevertheless, the productive zone reached below 25 m, where P^B was still significant.

(2) Spring (usually April and May; but varying for specific years): the spring phase started as soon as thermal stratification built up and lasted until the first major turbidity input limited productivity. As warmer water and available nutrients improved conditions for algal growth, stratification allowed a build-up of

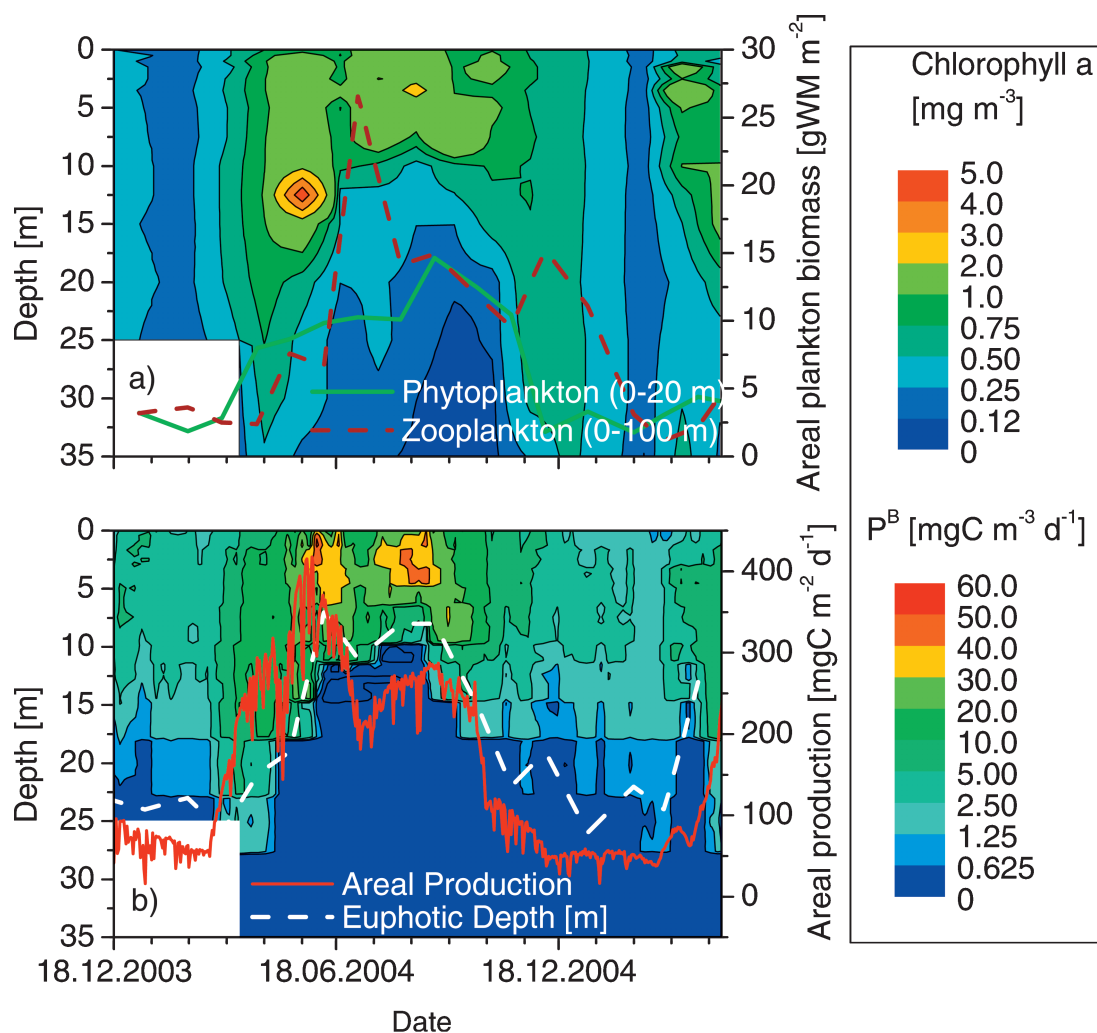


Figure 4. Primary production indicators in Lake Brienz from 18 December 2003 to 3 May 2005: a) Measured *in situ* chlorophyll a is shown as contour plot, based on monthly profiles. The solid green line illustrates phytoplankton (wet mass) in the top 20 m and the dashed red line denotes zooplankton (wet mass) in the top 100 m (data: net hauls by GBL). b) Calculated daily primary production (contour plot) based on 18 monthly C assimilation profiles. The solid red line illustrates the areal primary production (right scale) and the dashed white line indicates the euphotic depth (left scale; definition in text).

phytoplankton in the top 20 m. Consequently, relatively intense P^B of up to $20 \text{ mgC m}^{-3} \text{ d}^{-1}$ were observed at depths between the surface and $\sim 17 \text{ m}$, but P^B was negligible below 28 m . The areal primary production reached its yearly maximum of up to $400 \text{ mgC m}^{-2} \text{ d}^{-1}$ just before the summer phase (Fig. 4b).

(3) Summer (June – August): Allochthonous particle input from the two major inflows resulted in a turbid layer across the entire lake, causing enhanced light attenuation. The euphotic depth was reduced to a seasonal minimum of $\sim 8 \text{ m}$, limiting primary production to the uppermost layer. In the euphotic zone, P^B reached a maximum of up to $60 \text{ mgC m}^{-3} \text{ d}^{-1}$ at about 2 m depth, as photoinhibition hampered P^B closer to the surface. Despite longer day length ($\sim 11 \text{ h d}^{-1}$) and maximal phytoplankton densities, the areal primary production was $< 260 \text{ mgC m}^{-2} \text{ d}^{-1}$ (less than in spring).

(4) Autumn (September – November): During fall, allochthonous particle input decreased and, therefore, the lake cleared. The euphotic depth increased and P^B exceeded the detection limit down to a depth of 20 m . Shorter day length and convective mixing reduced P^B to $< 10 \text{ mgC m}^{-3} \text{ d}^{-1}$ in the entire euphotic zone, and consequently areal primary production decreased below $100 \text{ mgC m}^{-2} \text{ d}^{-1}$ (Fig. 4b).

The temporal integral over 2004 resulted in an annual gross primary production of $70 \text{ gC m}^{-2} \text{ yr}^{-1}$. This value reflects the ultra-oligotrophic state of Lake Brienz, as it lies well below the mean primary production of all the other measured peri-alpine lakes, such as Lake Lucerne ($\sim 160 \text{ gC m}^{-2} \text{ yr}^{-1}$) or Walensee ($180 \text{ gC m}^{-2} \text{ yr}^{-1}$) (Gammeter et al., 1996).

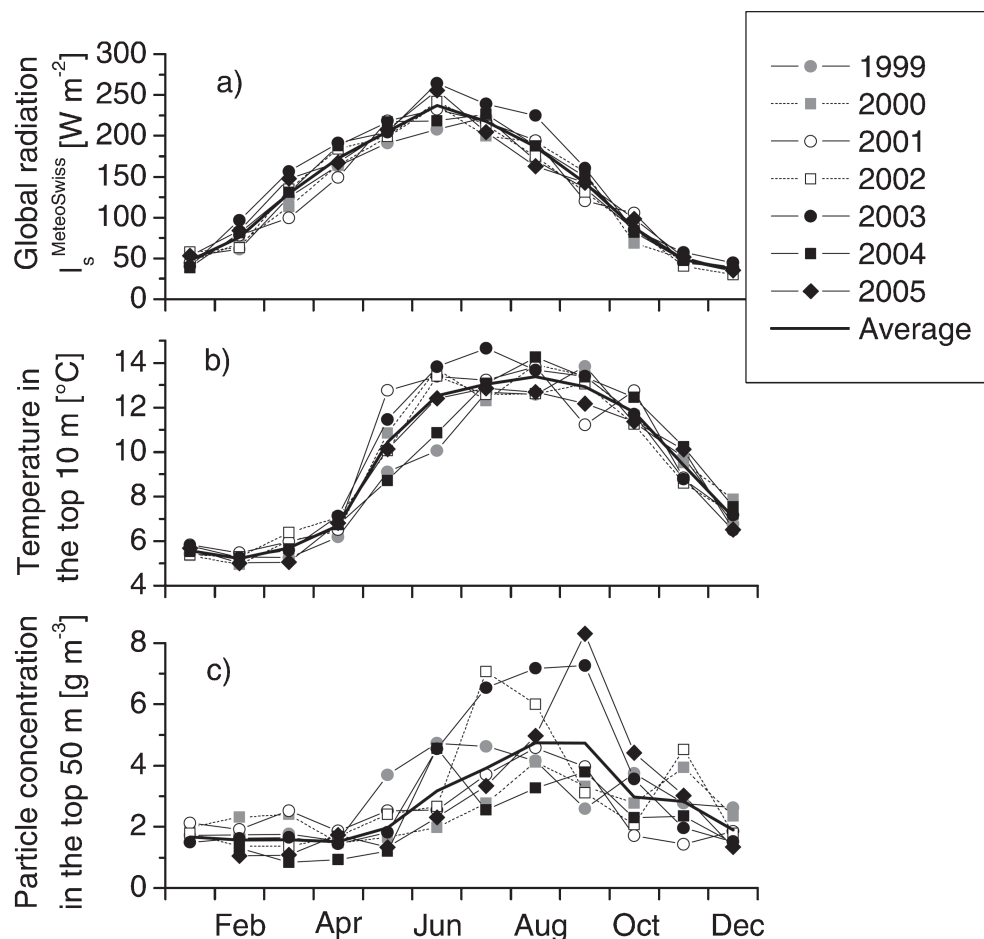


Figure 5. Physical conditions in Lake Brienz from 1999 to 2005: a) Monthly-averaged global radiation at Interlaken (location C; Fig. 1); b) Monthly average water temperature in the top 10 m; c) Average particle concentration in the top 50 m. Modified from Finger et al. (2006).

Physical boundary conditions during recent years

The average global radiation measured at location C (Fig. 1) was 132 W m^{-2} (Fig. 5a). In March and April 2001, global radiation was about 18% below average, and during the heat wave in August 2003 (Schär et al., 2004) it was about 20% above average. Although the extremely hot weather caused maximum temperatures in most Swiss lakes (LHG-BWG, 2005), significantly warmer water was recorded in Lake Brienz only in July 2003 (Fig. 5b). Two factors explain this anomaly: (1) the warm air temperatures led to intense glacial melting and subsequent cold inflows; and (2) intense turbidity – due to the high load of glacial particles – reduced light penetration and therefore limited warming at greater depths. This interesting mechanism protected the lake from extreme temperatures but also limited temperature-dependent primary production.

There were 3 periods when exceptional particle concentrations affected light availability (Fig. 5c): (1) the flood in spring 1999 led to high particle concentrations uncommonly early in the season, which

reduced light availability; (2) in 2003 exceptionally high particle concentrations were observed between July and September due to severe glacier melting as a result of the heat wave (Finger et al., 2006); and (3) after the extreme flood of 22 August 2005 (Beniston, 2006), record particle concentrations were observed.

Estimated primary production during recent years

As only temperature and light availability are considered in the model, differences among predictions for specific years may be directly attributed to the physical boundary conditions presented in Figure 5. The average annual gross primary production from 1999 to 2005 was estimated at $\sim 66 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Fig. 6a). Elevated particle concentrations during May and June 1999 led to $\sim 10\%$ lower primary production ($60 \text{ gC m}^{-2} \text{ yr}^{-1}$). Conversely, below average particle concentration and above average water temperatures led to $\sim 9\%$ higher primary production ($72 \text{ gC m}^{-2} \text{ yr}^{-1}$) in 2000. High particle concentrations and reduced light availability during the heat wave in 2003 led to $\sim 3\%$ below average primary production ($64 \text{ gC m}^{-2} \text{ yr}^{-1}$).

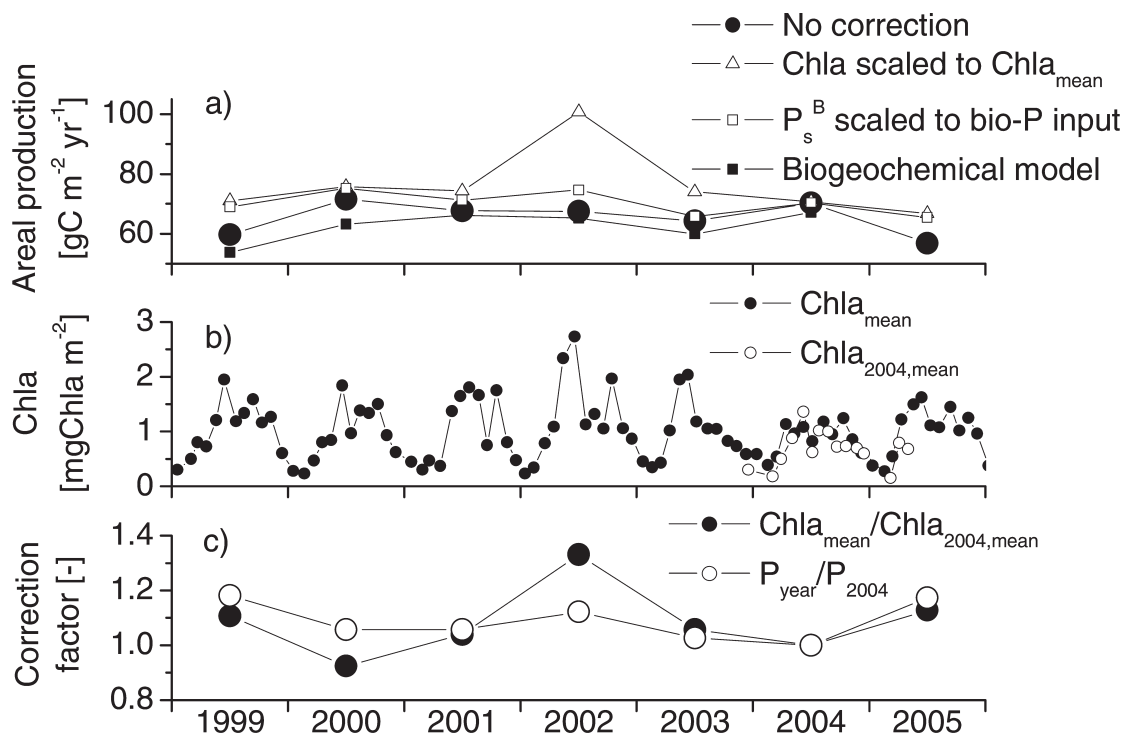


Figure 6. a) Predicted annual gross primary production from 1999 to 2005 compared to 2 test runs (see text) and a biogeochemical model described in Finger (2006); b) areal chlorophyll a concentration (GSA data) and mean concentrations during our sampling; c) correction-factors $Chla_{mean}/Chla_{2004,mean}$ (equation 5) and P_{year}/P_{2004} (equation 6).

The effects of the physical boundary conditions (Fig. 5) were even more pronounced when monthly averages were considered (Fig. 7). Excellent conditions in June 2000 with high radiation and low turbidity led to ~37% above average primary production. Low radiation and high turbidity led to ~22% below average primary production in May and June 1999. This minimum is important evidence for the collapse of the *Daphnia* population in 1999 (Rellstab et al., 2007). Finally, ~28% below average primary production was predicted just after the ‘flood of the century’ in August 2005 (Beniston, 2006).

The simulated time series of primary production was compared to the results of the biogeochemical model by Finger (2006) and the test runs with year specific $Chla(z, t_y)$ and bio-P input (Fig. 6a). Although the biogeochemical model has been calibrated with the primary production measured in 2004, it is an independent approach that considers bio-P input, temperature, light attenuation, vertical mixing, phyto- and zooplankton. The inter-annual primary production deviated by < 7% for specific years and showed an underestimation of only 4% for 2004.

The model test run with year specific $Chla(z, t_y)$ (equation 5) resulted in 16% higher average primary production because the observed $Chla$ concentrations were relatively low in the reference year 2004 (Fig. 6b). Gross primary production in 2002 was

predicted to be ~49% higher, primarily because of the up to ~60% above average $Chla_{mean}$ in May and June. However, there was no complementary evidence for increased production during this period, such as uncommon phyto- and zooplankton densities (Finger, 2006; Müller et al., 2007b; Rellstab et al., 2007), low turbidity, high bio-P input, or high global radiation (Figs. 5 and 6c). Thus, the higher value of $Chla_{mean}$ for 2002 may simply represent the natural variability within Lake Brienz. Furthermore, the $Chla$ scaling degraded the agreement with the biogeochemical model, indicating that light and nutrient limitation were more important driving variables for primary production than algal standing crop.

A test run with P_s^B scaled to annual bio-P input (equation 6) revealed 7% higher average primary production (Fig. 6a). This discrepancy can be attributed to the floods (e.g. 1999 and 2005) since bio-P input (P_{year}) was assumed proportional to water discharge (Finger, 2006). Disregarding the flood year and 2002 (unexplainable high $Chla_{mean}$) differences remain below 5%.

Our primary goal was to assess the effects of light and turbidity on productivity. For this reason we relied on the simulations that do not consider $Chla_{mean}$ or P_{year} . The additional test runs were performed to estimate the potential effects of these variables on productivity. Based on the results of the test runs, we

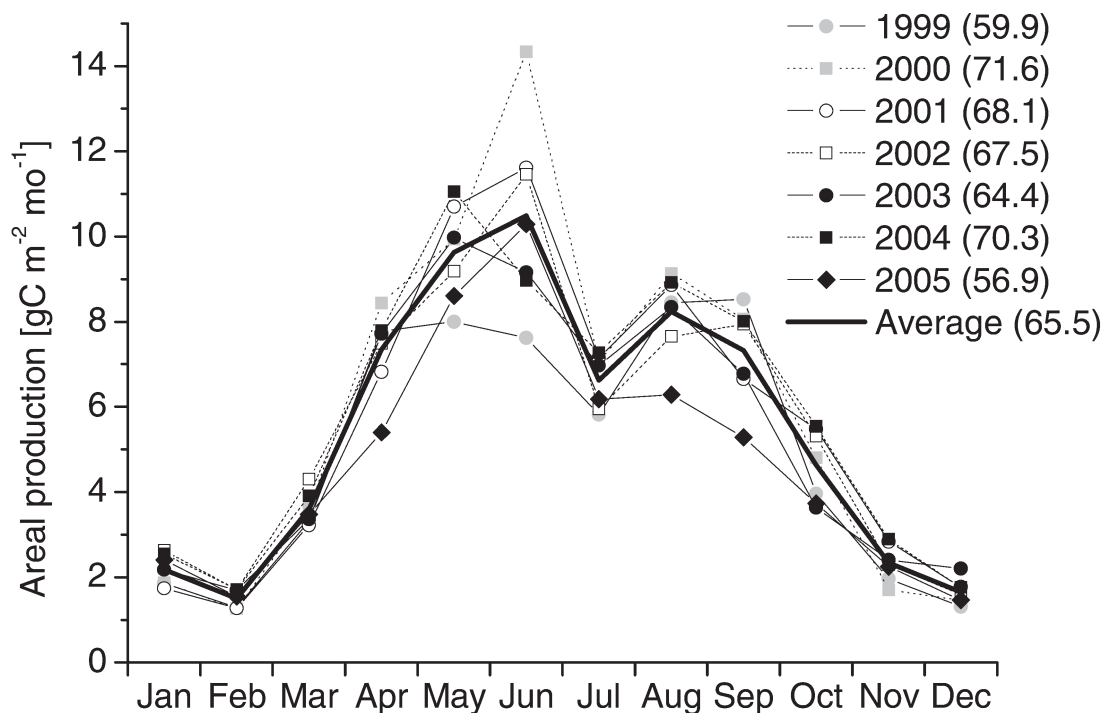


Figure 7. Predicted monthly gross primary production from 1999 to 2005 based on global radiation, PAR-profiles, water temperature, chlorophyll a and the monthly fits in 2004 (Fig. 2). Values in parentheses denote annual gross primary production ($\text{gC m}^{-2} \text{yr}^{-1}$) integrated for the year specified.

estimate the error of average annual primary production to $< 16\%$ (Fig. 6a).

Effects of turbidity on primary production

About 97% of the suspended particles entering Lake Brienz settle, and only 9 kt yr^{-1} are transported downstream to Lake Thun (Finger et al., 2006). Nevertheless, Lake Thun has a similar trophic status as Lake Brienz ($\text{SRP} < 1 \text{ mg m}^{-3}$ in spring). In recent years, the fishing yield in Lake Thun has been about twice as high as in Lake Brienz, indicating that turbidity might limit algal production and cause the difference in biomass output. To assess this hypothesis, we performed simulations of P^B for the light and temperature conditions of Lake Thun. *In situ* light availability was significantly higher (Fig. 8a); the euphotic depth reached $\sim 34 \text{ m}$ in winter ($\sim 24 \text{ m}$ in Lake Brienz) and decreased to $\sim 15 \text{ m}$ in summer ($\sim 7 \text{ m}$ in Lake Brienz). The lower turbidity and warmer inflows ($> 60\%$ stems from Lake Brienz with average temperature of $\sim 10^\circ\text{C}$) during summer led to almost 3°C higher water temperatures (Fig. 8b). Both higher euphotic depth and water temperatures enhance primary production.

Estimated areal primary production under the hypothetical turbidity-free conditions of Lake Thun would be $\sim 44\%$ higher ($\sim 95.3 \text{ gC m}^{-2} \text{yr}^{-1}$; Fig. 9) than in Lake Brienz. This increase is consistent with a

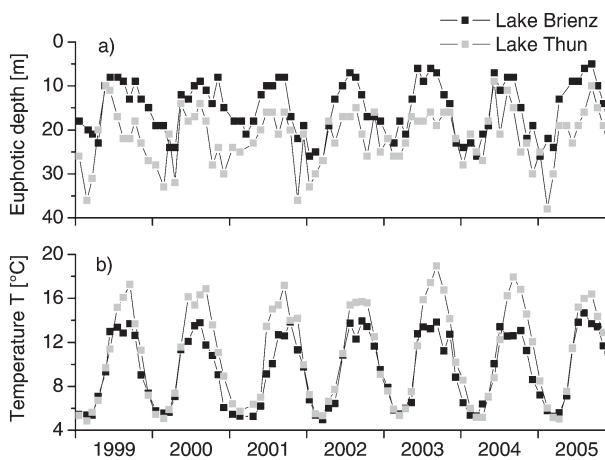


Figure 8. Euphotic depth (a) and average (top 10 m) water temperatures (b) in Lakes Brienz and Thun.

recent investigation of effects of glacial sediments on primary production in arctic lakes (Whalen et al., 2006), which indicated that primary production would be about two thirds higher without glacial sediments, especially during times of high turbidity (June – August). The minimum primary production in winter (January – May) would remain $\sim 25\%$ above the rates of Lake Brienz. The highest primary production ($\sim 23 \text{ gC m}^{-2} \text{mo}^{-1}$) for Lake Thun conditions would have been reached in June 2003 and June 2005, and minimal

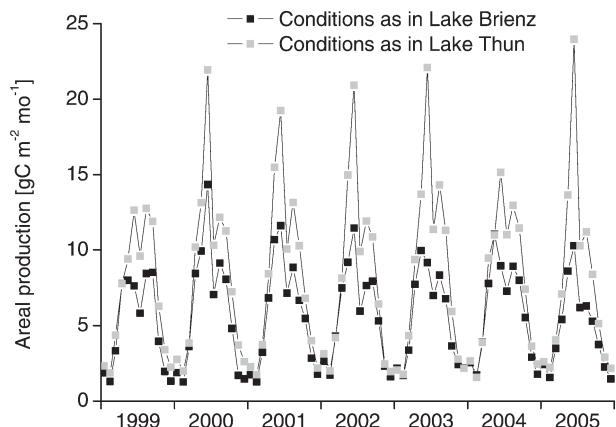


Figure 9. Predicted primary production under light and temperature conditions as in Lakes Brienz and Thun using the model based on the *in situ* primary production measurements in Lake Brienz.

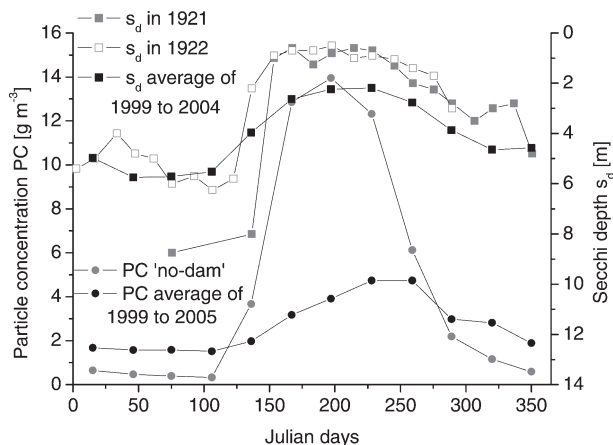


Figure 10. Secchi depth recordings (squares) for 1921 and 1922, as well as the average for the period 1999 to 2004 (right scale). Modelled average particle concentrations (circles) for today (1999 to 2005) and for 'no-dam' conditions (left scale) modified from Finger et al. (2006).

primary production (~11% below average; ~85 gC m⁻² yr⁻¹) would have occurred during the flood of 1999.

Effects of hydropower operations on primary production

Hydropower production decreased particle concentrations in the surface layer of Lake Brienz by almost ~50% during summer but increased them by ~100% during winter and spring (Finger et al., 2006). These findings are supported by time series of Secchi depths from 1921 and 1922 (Fig. 10), before the construction of the dams (Flück, 1926; Jaun et al., 2007). Using the correlations between Secchi readings (s_d), particle

concentrations (PC) and light attenuation (Jaun et al., 2007), we reconstructed the pre-dam light regime and estimated the corresponding primary production using T, *Chla* and $I_s^{MeteoSwiss}$ for the year 2004.

We compared primary production between 1999 and 2005 with primary production for 1921 and 1922 and the hypothetical 'no-dam' conditions (Fig. 11), assuming that bio-P input was similar (Müller et al., 2007a). The annual primary production under 'no-dam' conditions averaged ~12% (58 gC m⁻² yr⁻¹) below present conditions. Pronounced differences were noted from June to August, where pre-dam

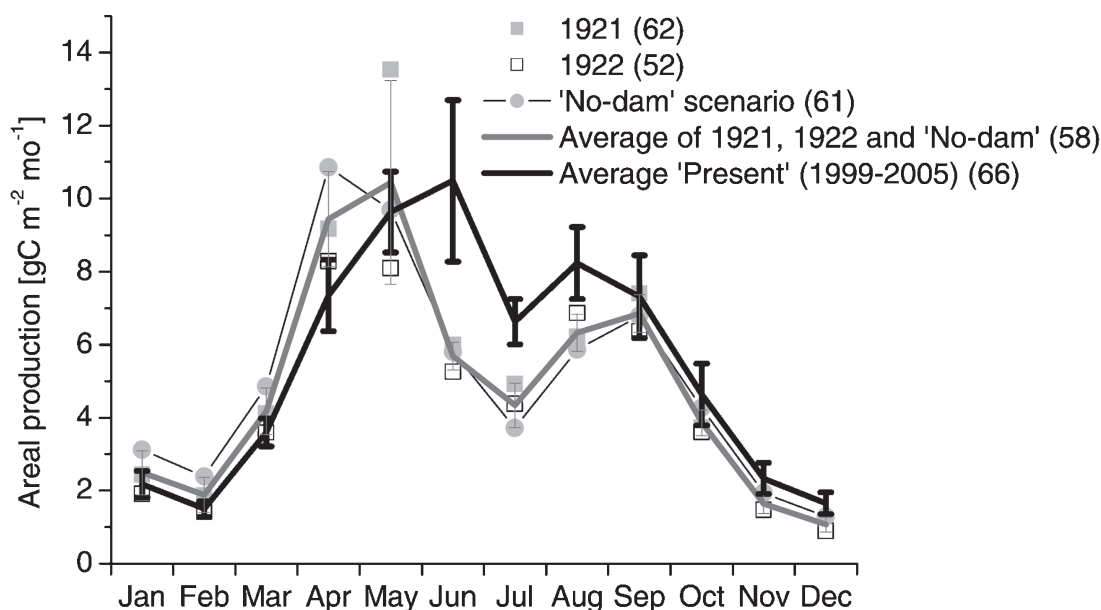


Figure 11. Predicted monthly gross primary production rates under present (1999 to 2005) and 'no-dam' conditions (1921 and 1922 is based on Secchi recordings before the construction of the dams). Error bars on the averages for present and 'no-dam' primary production indicate the standard deviations. Values in parentheses denote annual gross primary production (gC m⁻² yr⁻¹).

primary production estimates were ~35 % lower (~5.4 gC m⁻² mo⁻¹; more particles) than today (~8.4 gC m⁻² mo⁻¹; less particles). In contrast, lower light attenuation without dams increased primary production to ~4.5 gC m⁻² mo⁻¹ from January to May, which is about ~23 % higher compared to present (~3.6 gC m⁻² mo⁻¹). In comparison to the increase of primary production during summer the decrease during winter was 1.5 times weaker.

The most significant changes were observed in spring, when snowmelt and precipitation events led to turbidity intrusions in the lake. As is the case today, Secchi readings of 1921 and 1922 showed high inter-annual fluctuations (Fig. 10). The estimated primary production in May 1921 was ~50 % higher than average primary production in May today, whereas the estimated primary production in May 1922 remained ~28 % below the contemporary level. It is likely that before damming, fluctuations in turbidity were stronger than today, as the reservoir retention smoothes heavy rain runoff.

Discussion

Primary production depends on numerous biotic and abiotic factors, leading to uncertainties in model simulations. Temperature has little effect (equation 1) on model results because temperature-independent simulations ($Q_{10} = 1$) deviate < 5 %. This is consistent with a recent study by Staehr and Sand-Jensen (2006) and reveals the low sensitivity of model results to Q_{10} . The low SRP levels suggest a strong dependence of primary production on varying bio-P input and algae standing crop. During ordinary years, without floods (e.g. 1999, 2005) or unexplainable algae blooms (e.g. 2002), results of an additional simulation with year-specific algal standing crop or P_S^B scaled by bio-P input indicate that the effects of bio-P input or standing crop is < 15 %. In regard to the impacts of hydropower dams, the effects of light and turbidity on primary production are most relevant, and we therefore rely on the simulation that does not consider bio-P input or algal standing crop.

The simulated gross primary production in Lake Brienz amounted ~70 gC m⁻² yr⁻¹ in 2004, whereas primary production for 1999 to 2005 averaged ~66 gC m⁻² yr⁻¹. Müller et al. (2007a) estimated the net organic carbon mineralization rate at the deepest point of the lake at ~15.7 gC m⁻² yr⁻¹. This implies that organic carbon is recycled about 4 times per year, which lies within the range of typical values determined for oligotrophic lakes (Wetzel, 2001). The low gross primary production (about half of other peri-alpine lakes) is a consequence of low bio-P input, limiting the

intensity of primary production, and high turbidity, restricting primary production to the top layer of the lake.

Model simulations with light and temperature data from Lake Thun indicate ~44 % higher primary production if Lake Brienz was not affected by allochthonous particle input. Although primary production would still be very low, fishing yield and plankton time series of Lake Thun indicate that such a primary production rate could compensate for harsh conditions, such as the flood of 1999.

Increased turbidity during May and June 1999 decreased the simulated annual primary production in 1999 by ~10 %. High temperatures during the heat wave in summer 2003 stimulated primary production but also led to enhanced glacier melting and subsequently to an increase in particle input and light attenuation. Thus, these two opposing effects led to a ~3 % below average primary production in 2003. While these estimations seem realistic, primary production in 2005 was probably underestimated, as bio-P input must have been > 20 % above the 2004 level (Fig. 6b).

The reduced primary production in spring 1999, low water temperatures and high discharge provide a plausible explanation for the collapse of the *Daphnia* population (and subsequently fishing yield) in 1999. Rellstab et al. (2007) determined the mean intrinsic rate of growth of the *Daphnia* population in Lake Brienz to vary around 0.04 d⁻¹ in spring. Model calculations by Rellstab et al. (2007) indicate that reduced growth and increased flushing (due to higher throughflow) could lead to orders of magnitude lower *Daphnia* concentrations at the end of June. Nevertheless, no significant declines were observed in zoo- (i.e. *Daphnia*) and phytoplankton populations during the flood in August 2005. Test runs with P_S^B scaled to bio-P input indicate that the negative impacts of the flood 2005 were partially reversed by enhanced bio-P input. Furthermore, the *Daphnia* population in Lake Brienz is especially sensitive to reduced primary production at the beginning of summer when regeneration is necessary after the extremely low population density during the winter.

Although severe meteorological conditions may have led to the *Daphnia* collapse in 1999, the long-term decline in phyto- and zooplankton were not caused by short-term meteorological events. As the annual bio-P input today is comparable to the bio-P input prior to damming (Müller et al., 2007a), the changes in turbidity (Fig. 10) present the most significant effect of hydropower production. The model runs for 1921, 1922 and the modelled 'no-dam' scenario illustrate the effects of hydropower operation (Fig. 11). The annual primary production without

hydropower dams is estimated to be ~12 % lower than today. Primary production in summer under pre-dam conditions is predicted to be ~35 % lower than today. Yet, average primary production under 'no-dam' conditions between January and May is estimated ~23 % (~5.7 gC m⁻² mo⁻¹) above present primary production (~4.9 gC m⁻² mo⁻¹), at the time when regeneration of zooplankton is important. However, standard deviations of primary production rates in spring today and under 'no-dam' conditions overlap, making it difficult to determine consistent trends. Moreover, May and June 1922 can be identified as a high water event (discharge rates were 32 % above the average of 1910 to 1929), presumably with a particle load substantially above average. Consequently, Secchi readings from spring 1921 may be more representative for a typical pre-dam situation than those from 1922, suggesting that average 'no-dam' primary production in spring is underestimated. Thus, hydropower operations led to a temporal displacement of maximal areal primary production (Fig. 11) from May (during pre-dam conditions) to June (today). This time shift might be critical for the spring regeneration of zooplankton.

Conclusions

The effects of hydropower operations on primary production in downstream lakes were quantified by modelling primary production under the present light regime (1999 to 2005) and under 'no-dam' conditions. Furthermore, the model was used to estimate primary production in a hypothetical turbidity-free scenario, using temperature and light data from neighbouring downstream Lake Thun. From the *in situ* measurements and the numerical simulations the following conclusions can be drawn:

(1) Average annual gross primary production for 1999 to 2005 in Lake Brienz amounted to 66 ± 11 gC m⁻² yr⁻¹ (error was estimated with additional test runs). The low primary production can be explained by the exceptionally low SRP level (< 1 mg m⁻³) and strong light attenuation caused by allochthonous particles, especially during summer. The maximum areal primary production of up to 400 mgC m⁻² d⁻¹ is reached between May and June, when SRP is slightly higher and light availability is favorable. During summer, primary production is high (up to 60 mgC m⁻³ d⁻¹), but limited to the top 10 m of the water column by high turbidity. Consequently, areal primary production in summer (~270 mgC m⁻² d⁻¹) is substantially lower than during spring (~400 mgC m⁻² d⁻¹) but much higher than in winter (~50 mgC m⁻² d⁻¹).

(2) Upstream hydropower reservoirs have halved light attenuation during summer and doubled attenuation during winter (Jaun et al., 2007) and, as a consequence, the estimated primary production under 'no-dam' conditions was ~35 % lower in summer and up to ~23 % higher in winter compared to present conditions. Annual gross primary production is estimated at ~12 % below present. As shown by Finger (2006), these alterations are small compared to the effects of nutrient reductions due to sewage treatment in the last 30 years.

(3) The largest inter-annual variability in primary production were estimated in May and June (standard deviation: up to ~20 %), representing a critical period for zooplankton communities, based on their need to regenerate from the harsh winter. This became evident when a collapse of the *Daphnia* population and fishing yield occurred just after the flood in spring 1999 (Müller et al., 2007b). Low temperatures and elevated particle loads in the rivers reduced primary production in spring (May and June) to ~22 % below the long-term average, probably jeopardizing the regeneration of zooplankton (Rellstab et al., 2007). In contrast, the modelled primary production was reduced only ~10 % below average following the 'flood of the century' with exceptionally high particle concentrations in August 2005 (Beniston, 2006). As no decline in zooplankton was observed after this flood, it can be assumed that this period in summer is less critical for sustaining zooplankton populations.

(4) Simulations with light and temperature data from turbidity-free Lake Thun indicate that primary production would be ~44 % higher if Lake Brienz had a similar level of clarity as Lake Thun. Nevertheless, primary production would still remain at an extremely low level compared to other Swiss peri-alpine lakes.

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