

Research Article

Temporary collapse of the *Daphnia* population in turbid and ultra-oligotrophic Lake Brienz

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Abstract. The cyclical parthenogen *Daphnia* is a key species in aquatic food webs. Its abundance is influenced by environmental factors like food quantity and quality, predation, diseases, temperature and washout by discharge. In ultra-oligotrophic Lake Brienz (Switzerland), which is turbid from suspended glacial material, *Daphnia* density has continuously decreased since the 1990 s. In spring and summer 1999, during and after a severe flood, *Daphnia* density was below detection level, but the population recovered the following year. Simultaneously, a drastic two-year decline occurred in the yield of whitefish (*Coregonus* sp.), which mainly feed on *Daphnia*. Several hypotheses were tested to explain the collapse of the *Daphnia* population: a negative effect of the suspended particles, a covering of the diapausing eggs by sediment,

and a combined washout/temperature effect. A direct negative effect of the particles and covering of diapausing eggs could be excluded. According to model calculations, the spring growth of the *Daphnia* population could not compensate the washout losses, as it was limited by poor food conditions due to re-oligotrophication and reduced by extraordinarily low water temperatures. Moreover, ephippia abundance analysed from sediment cores was consistent with the process of eutrophication and re-oligotrophication and indicated that daphnids did not persist in the lake in the period before eutrophication (until 1955). Like most peri-alpine lakes in Europe, Lake Brienz has returned to its natural ultra-oligotrophic state and is now unable to support a large *Daphnia* population and fishing yield.

Key words. Washout; suspended particles; bottom-up effects; sediment cores; cladocera; flood.

Introduction

Daphnia (Cladocera) are filter feeders that play an important role in the food webs of many lakes: they graze mostly on phytoplankton and are a main food

source for planktivorous fish. Fluctuations in *Daphnia* populations can have large top-down as well as bottom-up effects. Whereas top-down effects have received much attention in the past (e.g. Elser and Goldman, 1991; Bürgi et al., 1999), direct bottom-up effects of daphnids have rarely been shown (Müller et al., 2007b). Understanding the mechanisms that influence *Daphnia* populations is therefore of great importance. Basically, the size of a population is the

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result of the net population growth rate, i.e., the difference between birth and death rate. Several environmental factors, biotic and abiotic, can affect these rates: food quantity and quality, water temperature, discharge (which leads to dilution due to washout), predation, parasites, etc. In this study, we analyzed the first four parameters in the context of a population collapse that happened in ultra-oligotrophic Lake Brienz in Switzerland. This lake is turbid from inorganic suspended particles coming from glaciers in its catchment. The influence of predation on the *Daphnia* population is described in Müller et al. (2007b).

Food quantity

Daphnids, due to their small size and short generation time, respond rapidly to changes in algal food density. One of the most important life history traits affected by food quantity is fecundity (Lampert, 1978) and, subsequently, birth rate (Paloheimo, 1974). Food quantity is primarily influenced by temperature, light availability and nutrients. Inorganic suspended particles increase the light attenuation and therefore decrease primary production (Jewson and Taylor, 1978; Krause-Jensen and Sand-Jensen, 1998). In most peri-alpine lakes of Europe, phosphorus is the limiting nutrient. In lakes with inorganic turbidity, some of the phosphorus can be bound to suspended particles and is hence prevented from being used for primary production (Müller et al., 2006). The most reliable parameter for measuring food quantity for daphnids is particulate organic carbon (POC), others are chlorophyll and biomass of phytoplankton (Müller-Navarra and Lampert, 1996).

As long as food conditions are good, *Daphnia* normally reproduce asexually, which results in juveniles being genetically identical to their mother. When food conditions get worse, they can switch to sexual reproduction (Korpelainen, 1989), resulting in diapausing eggs sheltered in an envelope called an ephippium (Zaffagnini, 1987). In stable habitats such as large lakes, sexual reproduction is less frequent since the over-wintering of asexual females seems to be a more optimal mechanism (Lynch, 1983). Because ephippia normally sink to the lake bottom, sediments represent egg banks (De Stasio, 1989; Hairston et al., 1996) that can function as biological archives (e.g. Keller et al., 2002; Jankowski and Straile, 2003). The hatching of juvenile daphnids from diapausing eggs, though not yet completely understood, needs abiotic stimuli like change in temperature or photoperiod that could be prevented by intense sedimentation of organic or inorganic particles (Gyllstrom and Hansson, 2004).

Food quality

Daphnids do not feed selectively within a certain size range (Demott, 1982), but they can either accept or reject the filtered material as a whole. They not only ingest algae, but can also assimilate bacteria (Kankaala, 1988) or the organic fraction of suspended particles (Gliwicz, 1986). The quality of the food is a crucial parameter and depends not only on morphology and size (Lürding and Van Donk, 1996), but also on the stoichiometry of C, N and P (Sterner and Elser, 2002), the content and nature of fatty acids (Brett and Müller-Navarra, 1997) and toxicity (Laurén-Määttä et al., 1997). For example, if the phytoplankton exhibits a C:P ratio of over 300:1, *Daphnia* growth is predicted to be lowered due to a direct deficiency of P (e.g. Urabe et al., 1997). As inorganic suspended particles overlap the size range of organic particles ingested by daphnids (0.5 to 40 µm, Lampert, 1987), they are ingested and have an influence on food quality. In alpine or peri-alpine lakes, suspended particles are transported from glacial regions by tributaries (Sturm and Matter, 1978; Bezing, 1987).

Several field studies have shown a negative correlation between suspended particle concentration and the abundance of planktonic cladocera or even total zooplankton (e.g. Adalsteinsson, 1979; Hart, 1986, 1987). In lakes with a high content of inorganic particles, copepods and rotifers are normally favoured over cladocerans (Adalsteinsson, 1979; Kirk and Gilbert, 1990). To our knowledge, only four studies exist about the effect of suspended glacial particles on cladocerans in oligotrophic lakes (Zurek, 1980; Zettler and Carter, 1986; Koenings et al., 1990; Rellstab and Spaak, in press), all other studies focus on shallow lakes or reservoirs, in which particles originate from resuspension of the sediment. Laboratory studies have shown negative effects (e.g. reduction of ingestion rate, fecundity, survival, fitness and population growth rates) of suspended particles on daphnids that were usually more pronounced when combined with low food conditions (Zurek, 1982; Arruda et al., 1983; Kirk, 1992). However, in some studies, low concentrations of suspended particles had a positive effect on daphnids when combined with low food quantities (Kirk and Gilbert, 1990; Hart, 1992).

Temperature

Like most aquatic organisms, daphnids are strongly influenced by the surrounding water temperature. Egg development time (generation time) is solely temperature dependent (Bottrell, 1975; Saunders et al., 1999) and it directly influences, in combination with clutch size, the birth rate of a population (Paloheimo, 1974).

Discharge

As daphnids are not able to influence their horizontal position in a lake and are transported passively by currents, a short retention time of the water during a flood could result in a dilution of the *Daphnia* population (washout). Both zoo- and phytoplankton density could be reduced but the effect is likely to be more severe on zooplankton than phytoplankton, as the generation time of the former is significantly longer (Wetzel, 2001). The effect of washout on the population size of daphnids or other zooplankton has rarely been investigated, and existing studies have focused mainly on reservoirs (Zurek and Dumnicka, 1989; Campbell et al., 1998; Seda and Machacek, 1998) and floodplains (e.g. Bozelli, 1994), but not large natural lakes. Washout was shown to be one of several important factors explaining variation in *Daphnia* density in a large reservoir (Dirnberger and Threlkeld, 1986). Moreover, studies on downstream drift of lake plankton showed a similar species composition in the stream as in the lake above (e.g. Campbell, 2002), except when water level and discharge were low (Jann and Bürgi, 1988).

Study system

Lake Brienz, situated in the front range of the Swiss Alps (at 564 m asl), is an ultra-oligotrophic system (SRP = 0.9 $\mu\text{g l}^{-1}$, P_{tot} = 3.0 $\mu\text{g l}^{-1}$, spring circulation values, Wüest et al., in preparation) with a volume of 5.1 km³, a surface area of 30 km² and a maximal depth of 259 m. Like in most Swiss lakes, production in Lake Brienz is phosphorus limited. Due to anthropogenic inputs, its phosphorus content increased until the late 1970 s. Since then it has continuously decreased due to nutrient input control (Müller et al., 2007a). The two major inflows, the rivers Aare and Lütschine, annually transport over 300,000 tons of suspended glacial material into the lake, leading to a maximum suspended particle concentration of 24 mg l⁻¹ (dry weight) in the epilimnion of the centre of the lake in summer (Finger et al., 2006). Normal concentration of suspended particles is 4–8 mg l⁻¹ in summer and 1–3 mg l⁻¹ in winter. This surface turbidity reduces light availability (Jaun et al., 2007) and subsequently hampers primary production (Finger et al., 2007). Only 3 % of this suspended material is transported through the outflow, the rest is deposited as sediment in the lake.

Heavy snowfall in winter 1999 resulted in a large amount of melt water running into Lake Brienz in April and May. Additionally, intensive rainfall during May and June led to the highest measured lake level and discharge in the 20th century (Wüest et al., 2007). From February to August 1999, daphnids were undetectable. Simultaneously, in the years 1999 and 2000, a drastic decline of over 90 % in whitefish

(*Coregonus* sp.) yield was observed. The disappearance of daphnids, the most important food organism of whitefish in Lake Brienz (at least in summer and autumn), was responsible for the poor fishing yield in these two years (Müller et al., 2007b). For more detailed information on the study system see Wüest et al. (2007).

Aims and hypotheses

The present study was part of an interdisciplinary research project investigating the ecological impacts of anthropogenic changes in Lake Brienz and its catchment, which is strongly influenced by hydropower operation (Wüest et al., 2007). Other research studies included particle transport and lacustrine sedimentation (Anselmetti et al., 2007), inorganic colloids (Chanudet and Filella, 2007), nutrients (Müller et al., 2007a), light regime (Jaun et al., 2007), primary production (Finger et al., 2007) and zooplankton-fish interactions (Müller et al., 2007b).

The main aim of our study was to test different hypotheses for the collapse of the *Daphnia* population in 1999. To put this collapse into a temporal perspective, to assess if a similar collapse could happen again, and to obtain data for model calculations of hypothesis 3 (described below), basic data on the population dynamics of *Daphnia* had to be acquired in two ways:

a) The density of ephippia in several sediment cores was determined to assess how the *Daphnia* population developed during the eutrophication and re-oligotrophication of Lake Brienz in the 20th century.

b) To investigate the more recent history of the *Daphnia* population and its food condition, zooplankton and phytoplankton samples from a routine sampling program (established in 1993) and water temperature measurements were analyzed. Additionally, earlier zooplankton samples from 1985 to 1987 (taken by Kirchhofer, 1990) were included.

To explain the extraordinary collapse in 1999, the following hypotheses were tested:

Hypothesis 1: Negative influence of suspended particles. Inorganic suspended particles have a negative influence on *Daphnia* fitness and subsequently population growth rate, especially when combined with low food concentration. During the flood, this led to the collapse of the *Daphnia* population. To test this hypothesis, we performed a flow-through experiment, exposing daphnids to different combinations of suspended particle and algae concentrations. Details of this experiment are described elsewhere (Rellstab and Spaak, in press), but as it is one of the main hypotheses, the main results are included and discussed here.

Hypothesis 2: Covering of diapausing eggs. Due to the flood and the large amount of suspended particles transported into the lake, the sedimentation rate in spring 1999 was elevated, covering the diapausing eggs and preventing daphnids from hatching. To test this hypothesis, we compared the proportion of ephippia containing eggs with sedimentation rates in different sediment layers.

Hypothesis 3: Washout. In 1999, growth of the *Daphnia* population could not compensate for the losses due to washout, which was extraordinarily high because of the high discharge. Moreover, the harsh winter and the short water retention time during the flood led to a reduced water temperature, slowing down population growth even more. As a consequence, the *Daphnia* density was below detection level. To test this hypothesis, we performed model calculations of spring population growth.

Material and methods

Analyzing the *Daphnia* population of the 20th century by sediment cores

Sediment cores were taken with a gravity corer (diameter: 63 mm) in March and November 2004 from two different locations (see Fig. 1 in Wüest et al., 2007): 1) cores BRZ1 and BRZ2: distal to the tributaries at a depth of 20 m (in the bay of Iseltwald); 2) core BRZ3: proximal to the tributary Aare at a depth of 190 m (near Brienz). The sediments of Lake Brienz are well investigated (Sturm and Matter, 1978): in the shallow area distal to the tributaries, sedimentation is low and constant. In the deep area proximal to the tributaries, sedimentation is high and mainly influenced by flooding and depositional events, and hence is highly variable. All cores were cut into 0.5 (BRZ1 and BRZ2) or 1.0 cm (BRZ3) slices. In BRZ1 and BRZ2, dating was done by measuring the clearly visible varves (using the image processing and analysis software Image-Pro Plus) and verified by determining the ¹³⁷Cs concentration of the different sediment layers (Appleby, 2001). In BRZ3 only the latter method could be applied. Sediment layers were sieved through a 250 µm mesh and ephippia in all layers were counted.

Routine sampling of *Daphnia*, phytoplankton and temperature from 1985 to 2005

Quantitative sampling of the daphnids was performed at least monthly from June 1985 to January 1988 and from December 1993 to December 2005 using a twin net with a mesh size of 95 µm, sampling the depth range of 0–100 m. Samples were preserved in 4%

formalin and densities of the daphnids were determined thereafter. Quantitative sampling of the phytoplankton (0–20 m) was performed at least monthly between December 1993 and January 2006 using an integrating sampler (Schroeder, 1961). Samples were preserved with Lugol's solution and counting was performed thereafter. From February 1994 to December 2005, water temperature profiles were measured monthly using a Seabird 19 CTD. All measurements described above were performed near the centre of the lake, at the location of maximum depth.

Negative influence of suspended particles (Hypothesis 1)

To test hypothesis 1, we performed a flow through experiment – as described in detail in Rellstab and Spaak (in press). In brief, we exposed juvenile daphnids from Lake Brienz to different concentrations of suspended particles (freeze-dried sediment material) and algae (*Scenedesmus obliquus*). After 6 days, mortality and several life-history traits (fecundity, length and juvenile growth rate) were measured to determine fitness.

Covering of diapausing eggs (Hypothesis 2)

To test hypothesis 2, we compared the proportion of ephippia with eggs (obtained from the cores described above) to the sedimentation rate (measurement described above) for different time intervals during the last century.

Washout (Hypothesis 3)

To test hypothesis 3, we performed model calculations. First, spring growth rates of the *Daphnia* population from years other than 1999 were determined by analyzing the quantitative data from routine sampling. These net growth rates were then used for parameter estimation. Second, the effect of elevated discharge and lower water temperatures in 1999 on the spring population growth was calculated.

The total density of daphnids normally shows an exponential growth from early spring to summer:

$$D(t) = D_0 \cdot e^{rt} \quad (1)$$

where $D(t)$ = total density (individuals m⁻²) of daphnids on day t , t = day of year, D_0 = virtual density at beginning ($t=0$) of the year (individuals m⁻²), and r = average net population growth rate (d⁻¹). By fitting an exponential curve to the density data during spring population growth, r and D_0 were estimated – using the least-square method – for each year from 1986 to 1987 and 1994 to 2005, except 1999.

The net population growth rate r is the difference between the instantaneous birth rate b and the total

death rate d (Paloheimo, 1974), which is a sum of predation, natural death (which are here both assumed to be constant when comparing years) and loss by washout (d_w). As the parameter r , defined above, already includes a certain loss due to washout in average years, we defined d_w (d^{-1}) as the difference between the loss in 1999 and the corresponding value for an average year on the same day of the year:

$$d_w(t) = \frac{Q_{1999}(t) - Q_{\text{average}}(t)}{V} \quad (2)$$

where Q_{1999} = discharge in 1999 ($\text{m}^3 \text{d}^{-1}$) at the outflow in Ringgenberg (see Fig. 1 in Wüest et al., 2007) on a specific day of the year (t), Q_{average} = discharge in an average year ($\text{m}^3 \text{d}^{-1}$, 1996 to 2005 without 1999) on the same day of the year, and V = volume of the upper 10 m (0.29 km^3). Discharge data from 1996 to 2005 were obtained from the Swiss Federal Office for the Environment (FOEN) and volumetric data from the Swiss Federal Office of Topography (Swisstopo). In our model we assumed that only the upper 10 m of the water column reach the outflow and that all daphnids are evenly distributed within this layer. Diel vertical migration (DVM, see Lampert, 1989; De Meester et al., 1999) was excluded for the following reasons: (1) juvenile daphnids in Lake Brienz do not migrate; (2) we did not observe DVM in 2005 in the same months when the flood occurred in 1999 (May and June), DVM started in July; and (3) a third of the adult *Daphnia* population does not seem to perform DVM (Ch. Rellstab, unpublished data).

A decreased water retention time should not only result in losses due to washout, but also in a reduced water temperature, as large amounts of cold water enter the lake in spring. This would reduce the instantaneous birth rate (b), which is negatively correlated with the temperature-dependent egg development time (Paloheimo, 1974). We therefore calculated a scaling factor (b_R) to account for the change in birth rate due to different temperatures in 1999, using the egg development times from Saunders et al. (1999). Water temperature data (average 0–10 m) from the monthly CTD profiles, linearly interpolated between sampling dates, were used.

Overall, we performed model calculations applying the following relationship:

$$\partial D(t)/\partial t = (b_R(t) \cdot r - d_w(t)) \cdot D(t) \quad (3)$$

using an average r over the whole time period and daily values for $d_w(t)$ and $b_R(t)$. For modelling the population growth of 1999, this would mean: If d_w is negative, the population would grow faster than assumed. If d_w is positive, but smaller than $b_R \cdot r$, the

population growth in 1999 would have been slower. If d_w is larger than $b_R \cdot r$, the *Daphnia* density would even decrease on this specific day due to washout. In this case, population growth could no longer compensate washout losses.

Results

Analyzing the *Daphnia* population of the 20th century by sediment cores

Based on ^{137}Cs dating, the sediment cores BRZ1 and BRZ2 showed an average sedimentation rate from 1963 to 2004 of 0.35 cm yr^{-1} . Much higher sedimentation rates were evident in core BRZ3; 1.14 cm yr^{-1} from 1986 to 2004 and 0.91 cm yr^{-1} from 1963 to 1986. The oldest layer analyzed for ephippia originated from approximately 1920. Figure 1 shows changes in ephippia abundance from around 1920 to 2004. Sediment core data of both locations show a good consistency: no ephippia were found from around 1920 to 1955 (BRZ1 and BRZ2) and 1930 to 1955 (BRZ3). After this period, ephippia were frequent, with two clear abundance peaks around 1960 to 1970 and 1980. In the beginning of the 1990 s, no ephippia were found for several years. Ephippia were present again from 1995 to 2004, but in lower densities than before.

Routine sampling of *Daphnia*, phytoplankton and temperature from 1985 to 2005

Figure 2 shows the total *Daphnia* density and total phytoplankton biomass during the long-term routine sampling. The density of *Daphnia* in Lake Brienz has been declining continuously since 1996. Winter and early spring densities have become especially low. During recent winters, a density below detection level (44 ind. m^{-2}) was usually observed for several months. However, in winter 2004 and 2005 daphnids were, despite their general absence in quantitative samples, always present in qualitative samples that represented a larger volume of filtered water (Ch. Rellstab, unpublished data). From 2003 to 2005 the *Daphnia* population of Lake Brienz consisted mostly of parental *D. hyalina* (normally 90% of adult females), but also hybrids between *D. hyalina* x *D. galeata* and their backcrosses could be found (Ch. Rellstab, unpublished data). Asexual gravid females were usually absent from January to April. The July peak of the population observed in the 1990 s does not occur or is only weakly pronounced since 2000. Sexual stages (females with ephippia and males) were almost always present in autumn. Maximum annual density has decreased from more $>150,000 \text{ individuals m}^{-2}$ in 1996 and 1997 to $<50,000 \text{ individuals m}^{-2}$ after 2003. The phytoplankton

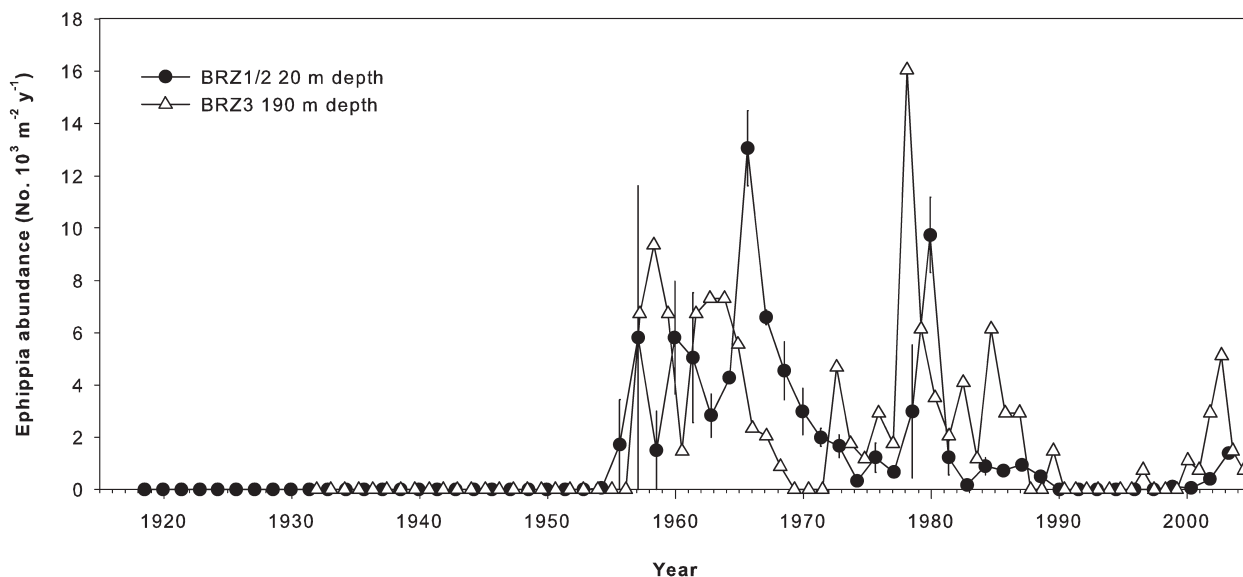


Figure 1. Abundance of ehippia in three different cores of Lake Brienz from approximately 1920 to 2004. Age of the sediment layers was determined by the ^{137}Cs -method. Error bars represent standard errors.

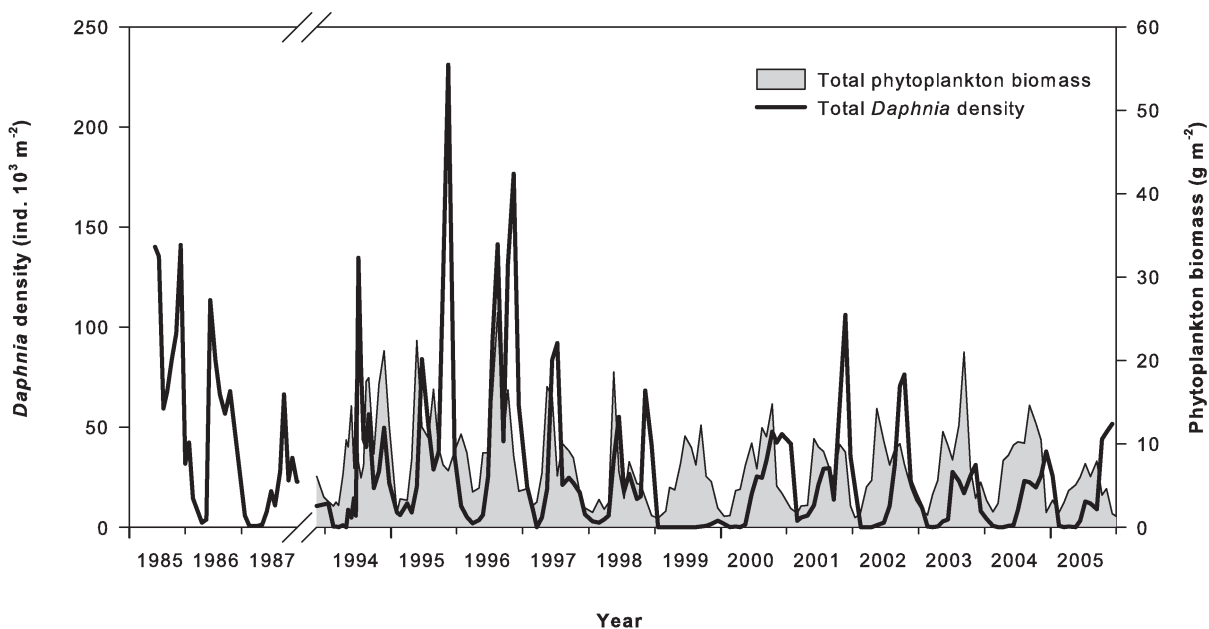


Figure 2. Total *Daphnia* density (line) and total phytoplankton biomass (grey shading, wet weight) in Lake Brienz from 1985 to 1988 and 1994 to 2005.

shows a similar trend, decreasing in biomass since 1996. After the usual density decline in January 1999, daphnids could not be detected in any zooplankton samples until September 1999. In contrast, phytoplankton biomass did not collapse and showed a normal annual pattern in 1999.

To compare between years, annual averages and averages between February and June (representing the period of the spring population growth) were calculated for total *Daphnia* density and phytoplank-

ton biomass (Fig. 3) from 1994 to 2005. Linear regressions showed a significant decrease with time in each of the following variables: annual average density of *Daphnia* ($r^2 = 0.35$, $p < 0.05$) and average *Daphnia* density between February and June ($r^2 = 0.35$, $p < 0.05$); annual average phytoplankton biomass ($r^2 = 0.41$, $p < 0.05$) and average phytoplankton biomass between February and June ($r^2 = 0.51$, $p < 0.01$). A positive correlation was found between the annual average *Daphnia* density and phytoplankton

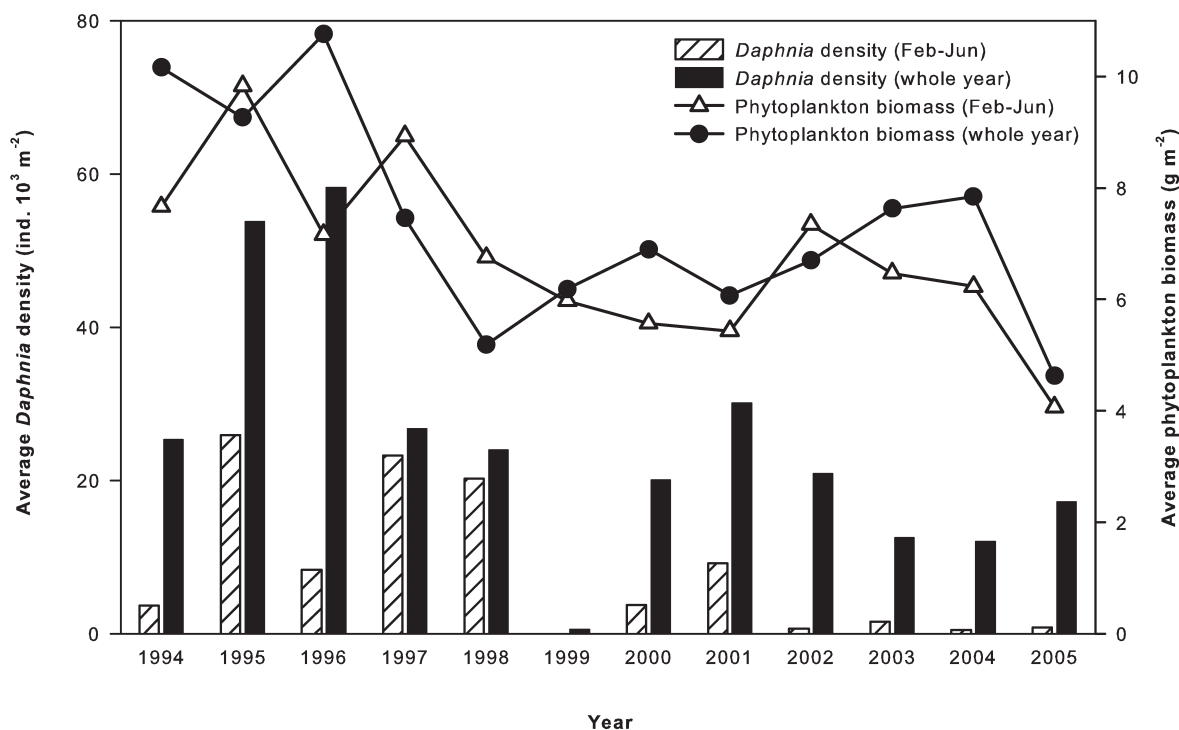


Figure 3. Average total *Daphnia* density (columns) and total phytoplankton biomass (lines, wet weight) in Lake Brienz from 1994 to 2005 for the whole year (black) and seasonally for February to June (white/cross-hatched).

biomass (Pearson's $r = 0.61$, $p < 0.05$, $n = 12$) and average *Daphnia* density and phytoplankton biomass between February and June (Pearson's $r = 0.70$, $p < 0.05$, $n = 12$). Average *Daphnia* density from February to June was around 25 times higher during the mid-90 s compared to after 2001. The ratio between annual average density and average density between February and June has increased considerably, from 1–6 to 20–30, indicating a delay in high density values towards later in the year. Phytoplankton biomass also decreased by 25–50% of the values measured in the mid-90 s, but the ratio between the period from February to June and the whole year has not changed.

Water temperatures in the upper 10 m from January to August were significantly lower in 1999 compared to the temperature in an average year (paired t-test, $p < 0.001$, $n = 8$): mostly the difference was between 0.2 and 1.2°C, the maximum difference of 2.6°C was found in June. Variation between years is normally low.

Negative influence of suspended particles (Hypothesis 1)

Detailed results are described in Rellstab and Spaak (in press). In summary, results showed that the concentration of suspended particles present in Lake Brienz does not reduce the fitness of daphnids, even at low food concentration. In fact, a low concentration of

suspended particles increased fitness. Reduction of fitness could only be observed at a suspended particle concentration of over 10–25 mg l⁻¹ and in combination with low food concentrations.

Covering of diapausing eggs (Hypothesis 2)

Sediment layers from the core proximal to the River Aare (BRZ3) contained a significantly higher proportion of ephippia with eggs (total mean: 41.2% ± 7.9 over the whole time period) than those from the cores distal to the tributaries (BRZ1/2, 13.4% ± 4.6) when comparing the same decades (paired t-test, $p < 0.01$, $n = 5$) (Fig. 4). Sedimentation rate of BRZ1/2, calculated by measuring varves and pooled into decades showed no significant correlation with the transformed proportion of ephippia with eggs of cores from the shallow and deep area (Pearson's correlation, $p = 0.79$ and $p = 0.21$ respectively, $n = 5$). Sedimentation rate in 1999 was below average at 0.20 cm yr⁻¹.

Washout (Hypothesis 3)

Table 1 shows the results of the regressions of the spring population growth in different years, where r represents an average net population growth rate during the exponential growth period in spring. With one exception (0.015 d⁻¹ in 2001), significant regressions always result in a net growth rate between 0.031

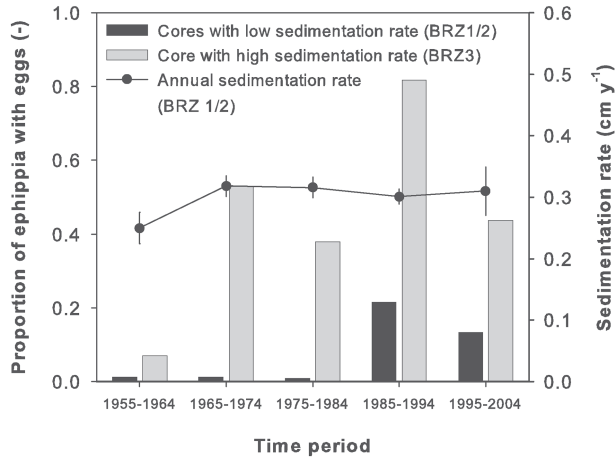


Figure 4. Columns: proportion of ephippia with eggs from areas with differing sedimentation rates in Lake Brienz in different decades: cores BRZ1 and BRZ2 (pooled) show low, and BRZ3 high annual sedimentation rates. Line: average annual sedimentation rate in cores BRZ1 and BRZ2, determined by measuring the clearly visible varves. Error bars represent standard errors.

Table 1. Results of the exponential regressions (Eq. 1) of total *Daphnia* density against time (day of year) in Lake Brienz from 1986 to 1987, 1994 to 1998 and 2000 to 2005 for months with exponential spring increase. r = average net population growth rate in the corresponding year; D_0 = virtual density at the beginning of the year. Months = months with exponential population growth included in the regression; Stars mark significant regressions (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Year	r (d^{-1})	D_0 (ind. m^{-2})	Months	R^2
1986	0.068	1.2	Apr – Jun	0.83
1987	0.032	34.8	Mar – Jul	0.93*
1994	0.032	46.1	Feb – Jun	0.61*
1995	0.020	1669.1	Feb – Jun	0.74
1996	0.035	61.1	Mar – Jul	0.95***
1997	0.094	0.04	Mar – Jun	0.87
1998	0.031	322.6	Feb – Jun	0.94***
2000	0.042	6.5	Feb – Jul	0.91***
2001	0.015	1290.6	Feb – Jul	0.97***
2002	0.041	1.9	Apr – Sep	0.97***
2003	0.045	4.6	Mar – Jul	0.97***
2004	0.040	3.3	May – Aug	0.94*
2005	0.048	3.1	Apr – Jul	0.78

and $0.045 d^{-1}$. These growth rates do not show any trend in time (linear regression, $r^2 = 0.03$, $p = 0.61$).

During May and June 1999, losses due to washout (d_{1999} , see Eq. 2) were always higher than $0.03 d^{-1}$ and reached a maximum of $0.08 d^{-1}$ on May 15th, implying that 8% of the upper 10 m were exchanged within 24 h (data not shown). Such a high water exchange rate was only observed for one other period (flood in August/September 2005, over $8\% d^{-1}$ in the upper 10 m) in the record span for the lake. Compared to average, the loss due to washout in 1999 (d_w , see Eq. 2) was higher for almost two months (April 21st to June 17th), reaching a maximum difference of almost $0.06 d^{-1}$ on May 15th (Fig. 5). Values of b_R (temperature scaling

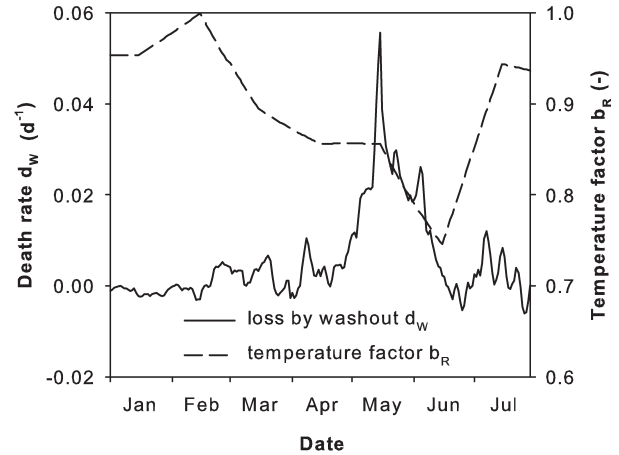


Figure 5. Data used for the model calculations. Solid line: increased death rate due to washout calculated from the discharge (data: Federal Office for the Environment, FOEN, Switzerland). Dashed line: temperature factor representing the reduction in birth rate, calculated from the average water temperature in the upper 10 m. Values of both parameters are shown as the difference of 1999 and the average from 1996 to 2005 (without 1999).

factor for growth rate r) were always below 1 until the end of August, reaching a minimum of 0.75 in the middle of June 1999, thus reducing the birth rate (and therefore r) by 25% (Fig. 5).

Based on the information obtained above, we modelled growth from a low, but realistic (see Table 1) virtual starting density (D_0 , see Eq. 1) of 5 individuals m^{-2} , using three different net population growth rate scenarios: high ($0.06 d^{-1}$), average ($0.04 d^{-1}$) and low growth rate ($0.02 d^{-1}$). Figure 6 shows the model calculations for 1999 (solid line) of the three different scenarios compared to the corresponding average net spring growth assuming average conditions (dotted line). In all scenarios, compared to average, the modelled 1999 population size was already smaller before the flood started, as the reduced water temperature led to lower birth rates. Using the high growth rate scenario ($r = 0.06 d^{-1}$, Fig. 6a), growth becomes negative only on May 15 if the elevated discharge and reduced temperature are applied. Growth is slower over the whole time period, but the population still reaches a high number of individuals at the end of June ($25,000 ind. m^{-2}$). Using the average growth rate scenario ($r = 0.04 d^{-1}$, Fig. 6b), the negative effect of washout and temperature is more pronounced. During five days (around May 15) the net growth is negative when the 1999 conditions are applied. The population needs 8 additional days to reach the original size again. The calculated population size at the end of June – $1,000 ind. m^{-2}$ – is small and considerably depressed compared to the value of 7,000 if no negative effects of increased washout and reduced temperature are applied. Using the low

growth rate scenario ($r = 0.02 \text{ d}^{-1}$, Fig. 6c) results in a period of almost 5 weeks with negative growth around the middle of May 1999. Recovery of the population to the same size takes almost another 4 weeks. At the beginning of July, the *Daphnia* density is around 40 individuals m^{-2} , which would still be below the detection level of the routine sampling. The scenario with the low growth predicted the observed data the best.

Discussion

History of the *Daphnia* population in Lake Brienz

Our analyses of several dated sediment cores show that *Daphnia* ephippia were produced extremely rarely or not at all between around 1920 and 1955 (Fig. 1), suggesting that daphnids were not present during that time period. Thereafter, with the exception of the first half of the 1990 s, ephippia were always present in cores, with two distinctive peaks in abundance: between 1960 and 1970, and around 1980. Basically the abundance of ephippia in the sediment showed a similar pattern as the reconstructed total phosphorus concentration for the same time period (Müller et al., 2007a), although the peaks are shifted in time. This indicates that the size of the *Daphnia* population in the lake, which normally increases with increasing P concentration up to a certain threshold (Lampert and Sommer, 1999), is the most important parameter determining ephippia abundance in the sediment (Keller et al., 2002; Jankowski and Straile, 2003). Still, we must be careful in analyzing the abundance of ephippia in the sediment, as it is also influenced by taxa composition (Jankowski and Straile, 2003; Keller and Spaak, 2004) and possible pre- and post-mating barriers (Keller et al., in press).

The presence of ephippia during a certain period implies the concurrent existence of *Daphnia*, but not necessarily vice versa, as it could also be the case that *Daphnia* are present but do not produce ephippia. However, there is strong evidence in the historic literature that daphnids were absent or very rare during that time: in all but one publication (Heuscher, 1901) daphnids were either not mentioned (Lutz, 1878) or described as not present (Burckhardt, 1900; Flück, 1926; Wuhrmann and Corti, 1947). Still, due to the asexual reproduction of the daphnids, even a population with a low density could persist for a longer period without being detected by the conventional plankton nets. Nevertheless, in the case of Flück (1926), no single *Daphnia* was found in 500 samples collected during two years. Considering all available data, it appears likely that daphnids did not establish themselves permanently in the lake before 1955.

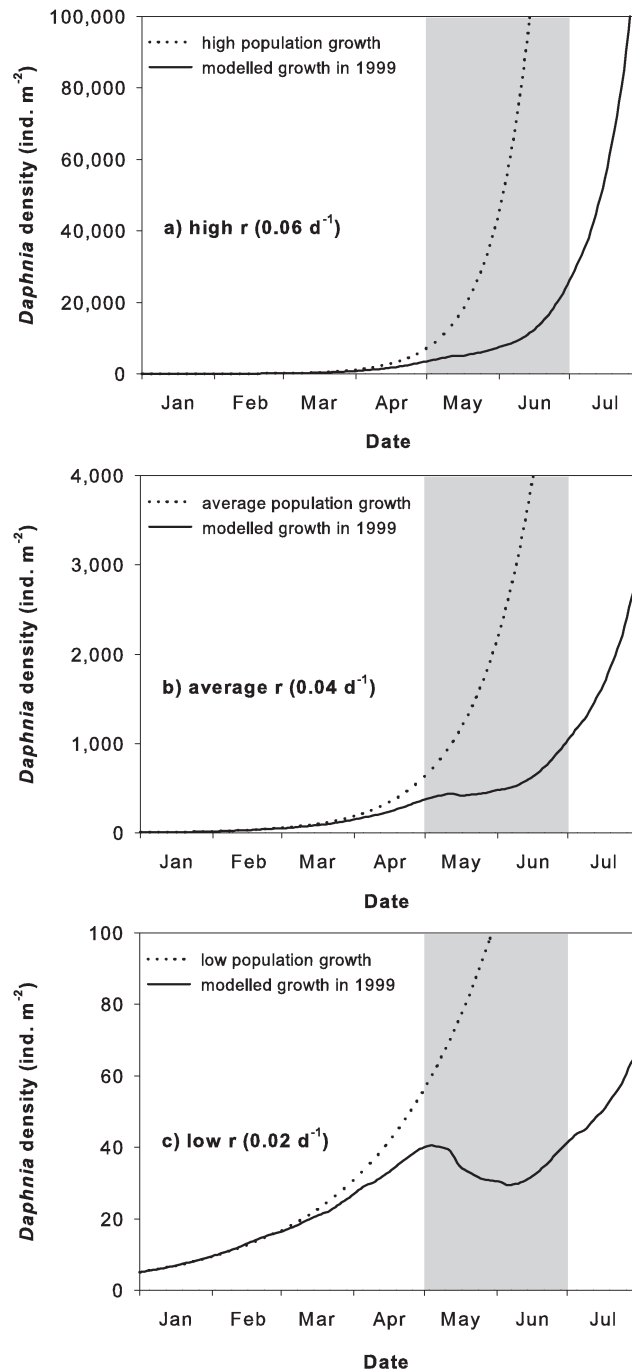


Figure 6a-c. Modelled spring population growth in Lake Brienz in 1999 with different growth rates (a-c). Dotted line: Modelled *Daphnia* density with average discharge and average temperature. Solid line: Modelled *Daphnia* density with elevated discharge and reduced water temperature of 1999. The grey shading shows the period of the flood. Note the different scales on the y-axes.

The results of our routine sampling showed that the *Daphnia* population has been decreasing over the last 11 years (Figs. 2 and 3). The average size of the population has recently declined to less than a third when compared to years with the highest

densities in the mid-1990's. Fishing yield data (Müller et al., 2007b) and the abundances of ephippia in the sediment (Fig. 1) indicate that the *Daphnia* density must have been even larger during the 1970 s. In winter, densities have been below detection level for several consecutive months in recent years. However, we know from qualitative samples that a part of the *Daphnia* population overwinters as asexual females. Nowadays, the population needs more time to reach the annual maximum size compared to the 1990's. The July peak of the population observed in the 1990's is rarely pronounced since 2000. It is possible that this shift is a consequence of a change in the taxa composition in the lake: in Lake Constance, *D. galeata* is known to have its density peaks in summer and *D. hyalina* in autumn (Jankowski and Straile, 2004). However, the hatching of diapausing eggs from the sediment cores under laboratory conditions does not reveal any evidence for the existence of a different taxa in the past (Ch. Rellstab, unpublished data).

Overall, the general decline of the *Daphnia* population is correlated with the decline in phytoplankton biomass (Fig. 3), which is again a consequence of the declining phosphorus content (Müller et al., 2007a). Moreover, although we lack C:P ratio data of phytoplankton in Lake Brienz, it can be assumed that, as a consequence of the reduction of phosphorus input, the C:P ratio has increased in the past. Since daphnids are sensitive to a high C:P ratio (Gulati and DeMott, 1997), food quality in terms of stoichiometry is therefore also a possible explanation for the decreasing population size. Inorganic suspended particles cannot be responsible for the decline, as their concentration is too low to lower daphnid fitness (Rellstab and Spaak, in press). Moreover, the particle content of Lake Brienz has not increased during the considered time period. The particle concentration is subject to strong interannual fluctuations, influenced by meteorological conditions such as flooding or intense glacier melting (Finger et al., 2006). Interestingly, the density of copepods (mainly *Eudiaptomus gracilis*) has not decreased that dramatically in the past. They are the dominating zooplankton species in the lake, but not a major prey for whitefish (Müller et al., 2007b). As *Eudiaptomus* is characterized by lower food threshold concentrations, they are better adapted to the food conditions in oligotrophic lakes (Lampert and Muck, 1985).

POC measurements in 2004 and 2005 showed that the average POC concentration from 0–10 m is below 0.1 mg C l^{-1} from December to April (Rellstab and Spaak, in press). Even from May to November, POC content is still low (max. 0.35 mg C l^{-1}), indicating that

food limits the growth of the *Daphnia* population all year. If we combine these data with the results of the quantitative sampling shown here, the food threshold level – inferred from females with eggs present or population growth – lies between 0.08 and 0.16 mg C l^{-1} . This is comparable to previous laboratory or field studies with similar *Daphnia* species (Lampert, 1978; Müller-Navarra and Lampert, 1996).

The collapse in 1999 (Hypotheses 1–3)

The collapse of the *Daphnia* population in Lake Brienz cannot be explained by the observed decline in food level alone. Monthly phytoplankton data show no extraordinary low algal biomass in 1999, neither for the period from February to June nor for the whole year (Fig. 3). No changes in the phytoplankton composition (regarding species or size classes) compared to other years were observed (data not shown here). However, these measurements were performed only monthly and are a good measure for food quantity but not quality. Model calculations of *in-situ* primary production, based on light attenuation data, indicate that elevated turbidity and low water temperature led to a reduction of 11% in phytoplankton growth for the year 1999 overall and a reduction of 23% for May and June compared to the average (Finger et al., 2007).

Inorganic suspended particles could also be excluded as a direct cause for the collapse in 1999 (Hypothesis 1). In a flow-through experiment described in Rellstab and Spaak (in press) we show that the concentration normally found in Lake Brienz ($1–8 \text{ mg l}^{-1}$, Finger et al., 2006) does not reduce, but actually increases the fitness of daphnids. Negative effects were only observed with a suspended particle concentration higher than $10–25 \text{ mg l}^{-1}$ and in combination with very low food levels ($0–0.1 \text{ mg C l}^{-1}$). This is in agreement with most laboratory studies, where a particle concentration below 50 mg l^{-1} normally had no negative effect (e.g. Zurek, 1982; Arruda et al., 1983; Kirk, 1992). Such a high concentration rarely occurs in Lake Brienz (maximum concentration measured is 24 mg l^{-1} in August 2005, Finger et al., 2006). Moreover, the highest inorganic particle concentration is normally found in summer at the same time as the highest POC concentrations (Rellstab and Spaak, in press). In 1999, the period with increased particle content in the upper layer of the lake (from April to September) was exceptional rather than the concentration of suspended particles (max. 6 mg l^{-1}). In fact, longer periods of turbidity outside the range of harmful concentrations can even have a positive effect on *Daphnia*, as the reduced water transparency lowers the reactive distance of visually hunting planktivorous fish (Vinyard and O'Brien, 1976; Carvalho, 1984) and

hence predation pressure. Daphnids are on average larger in lakes with high than in lakes with low turbidity (McCabe and O'Brien, 1983; Zettler and Carter, 1986).

In 1999, sedimentation in the shallow area distal to the tributaries was lower compared to average years, which allows us to reject hypothesis 2 proposing that an elevated sedimentation prevented daphnids from hatching. The place where ephippia sink to the lake bottom is of great importance: in the area with high sedimentation and missing hatching stimuli (like changes in day length and temperature, see Gyllstrom and Hansson, 2004) the proportion of ephippia with eggs was significantly higher than in the area with low sedimentation and hatching stimuli present (Fig. 4). Obviously, the sedimentation rate in shallow areas distal to the tributaries is not high enough to prevent daphnids from hatching the following spring. However, shallow regions in Lake Brienz are rare, 92 % of the lake area is deeper than 20 m. Ephippia with eggs that sink to these deep regions will most likely not hatch due to the reasons mentioned above.

Our model calculations of the spring population growth of 1999 provide a plausible explanation for the collapse in 1999, i.e., a combined temperature/washout effect (Hypothesis 3). Due to the low water temperatures before, during and after the flood, and a high discharge for several weeks, the growth of the *Daphnia* population, limited by poor food conditions, could not compensate losses due to washout. The population size remained low and no individuals were detected in zooplankton samples until September. Assuming that all other factors, except discharge and temperature, were similar to an average year, it would have taken 8 days for the *Daphnia* population to recover from a 5 day period of extremely high outflow. From the beginning of May to the middle of June, the population size would have only increased by a total of 40 % compared to 600 % in an average year with a daily net growth rate of 4 %. The combined temperature/washout effect can have drastic consequences if we consider the low growth rate scenario (assuming a daily population growth rate of only 2 %): the population would have decreased in density during the most extreme period of the flood for almost 5 weeks and grown only 2 % in total during May and June. Total daphnid density would not have reached the detection level (44 ind. m⁻²) until July. Besides the fact that this scenario predicted the observed data the best, there is more evidence that it is the most realistic one for 1999: As mentioned above, Finger et al. (2007) found a significant reduction in primary production in 1999 and for the period of the flood. Moreover, the predation rate of whitefish in Lake Brienz can reach values of several percent per day. Although predation

can be excluded as the main factor responsible for the population collapse, Müller et al. (2007b) found an elevated predation pressure in 1999 compared to average.

In contrast to spring 1999, the severe flood that happened at the end of August 2005 had no negative impact on the *Daphnia* population of Lake Brienz. This is not surprising, as the circumstances of this flood were completely different. In August 2005, the *Daphnia* population had already established itself and >60 % of the adult females had eggs. There were only 2 weeks of elevated outflow (compared to 9 weeks in 1999) and the higher water temperatures led to a higher birth rate compared to spring. Taking these facts into account, washout was not a significant factor since the birth rate could compensate for the washout losses. Moreover, a flood in summer is thought to transport more organic carbon than one in spring, an energy resource that the daphnids are likely to use (Gliwicz, 1986). The timing of a flood therefore seems to be crucial.

Implications for the future

Recent analyses predict that the global hydrological cycle, due to global warming, will intensify in the future, likely resulting in more extreme and more frequent floods (Huntington, 2006). Moreover, water runoff peaks of rivers dominated by snow or ice melt are supposed to take place earlier in the year (Barnett et al., 2005). A spring flood as in 1999, combined with intensive snow melting, is therefore likely to occur again and even more frequently in the future. Consequently, the probability of a collapse of the *Daphnia* population like in 1999 will increase. Moreover, if spring growth rates decrease in the future as a consequence of the ongoing decline in nutrient input and primary production, the population will be even more susceptible to environmental factors such as high discharge. However, it is unlikely that the *Daphnia* population is going to disappear from Lake Brienz permanently, as the population can re-establish from diapausing eggs every spring, a strategy that will increase in significance in the future.

Conclusions

In this study, we showed that the temporary collapse of the *Daphnia* population that happened in 1999 in turbid and ultra-oligotrophic Lake Brienz was likely caused by a combined temperature/washout effect, based on poor food conditions. In general, *Daphnia* densities have decreased in the last 11 years as a consequence of declining primary production. Sediment analyses and a literature survey strongly suggest

that daphnids were most likely absent from Lake Brienz before 1955. Considering additional data on production of different trophic levels (Finger et al., 2007; Müller et al., 2007a; Müller et al., 2007b), our results suggest that, after a modest period of eutrophication, Lake Brienz is returning to its natural ultra-oligotrophic state, with a small *Daphnia* population and low fishing yield.

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