

This is an Accepted Manuscript of the following article:

Susanne C. Schneider. Greener rivers in a changing climate?—Effects of climate and hydrological regime on benthic algal assemblages in pristine streams. *Limnologica*.

Volume 55, 2015, pages 21-32, ISSN 0075-9511.

The article has been published in final form by Elsevier at

<http://dx.doi.org/10.1016/j.limno.2015.10.004>

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Greener rivers in a changing climate? – Effects of climate and hydrological regime on benthic algal assemblages in pristine streams

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Keywords

Cyanobacteria; *Phormidium*; green algae; temperature; discharge; biodiversity; biomass; reference conditions

Abstract

Excessive biomass development of benthic algae is often considered undesirable, but understanding the causes is confounded by complex interactions among driving factors. Pristine rivers allow a benchmark where human interference should be limited to climate change. In this study a time series comprising > 20 years of annual benthic algae surveys from two pristine, soft water, boreal stream sites is used to determine whether year-to-year variations in benthic algal assemblages and cover were related to climate (temperature, precipitation, North Atlantic Oscillation) or hydrological regime. Total benthic algal cover ranged from 6 to 100% at Atna (the outflow of the Atna River from Lake Atnasjø), and from 3 to 50% at the headwater stream Li. Climate and hydrological regime explained 18 - 74% of the variability in benthic algal assemblages and cover. Generally, more variance was explained at Li than at Atna, possibly because i) aquatic bryophytes blurred nutrient-mediated effects of climate and hydrology at Atna, and ii) the upstream lake buffered hydrological variation. Temperature was more important for explaining benthic algal assemblages and cover at Atna, while hydrology was more important at Li. Climate and hydrological regime had no major impact on benthic algal taxon richness. High temperatures were associated with high benthic algal cover, particularly at Atna, while high suspended particle concentrations were associated with reduced benthic algal cover at Li, possibly due to scouring. Cover of the cyanobacterium *Phormidium* sp. increased at Li with increasing temperature, and decreased with prolonged periods of high discharge. Current predictions of climate change would lead to a “greener” Atna (increased cover of benthic algae), while Li would become more “bluegreen” (more *Phormidium* sp. but less filamentous green algae). It would also lead to a slightly more “eutrophic” algal assemblage at Atna (as indicated by the PIT-index for ecological status assessment), while a possible drift of the PIT-index is less clear at Li. The differences between Atna and Li likely reflect differences among river types, and it seems possible to make some generalizations: climate will likely affect benthic algae in lake outlets primarily via temperature, while headwater streams will primarily be affected via altered hydrology and particle concentrations.

1. Introduction

Benthic algae are an important part of riverine food webs. Their excessive biomass, however, is regarded undesirable, such that effective river management requires knowledge of what controls benthic algal growth. In addition to light (McIntire and Phinney, 1965), the most important abiotic parameters shaping benthic algal assemblages and biomass in streams generally are water quality parameters, e.g. particle concentrations (Piggott et al., 2015), nutrient supply and pH (Schneider et al., 2013), hydrological regime (Hart et al., 2013), and temperature (Bowman et al., 2007). The impact of these variables on benthic algae has been tested in experiments (e.g. Piggott et al. (2015); see Larned (2010) for a review of earlier studies), but these can only provide information about short-term effects. Long-term effects of climate and hydrological regime on ecosystems are notoriously difficult to predict, partly because we often lack knowledge with respect to the long-term adaptability of different species (Bellard et al., 2012), but also due to the manifold interactions among different functional groups and among different stressors (Piggott et al., 2015), which greatly complicates predictions of net responses of ecosystems. For ecosystems in cultural landscapes it is often difficult to disentangle the effects of climate or hydrology from those of other stressors, because they are often masked by concomitant land-use changes and nutrient loss from their catchments (Jeppesen et al., 2014).

Climate and hydrology exhibit short-term variations and long-term trends. Long-term climate change scenarios foresee, amongst other effects, an increase in temperature, a decrease in spring snow cover and an increase in frequency and intensity of heavy precipitation events in the Northern Hemisphere (IPCC, 2013). Nordic rivers are expected to experience earlier spring floods (Minville et al., 2008), a decrease in magnitude of low flows and an increase in magnitude of high flows (Fowler and Kilsby, 2007). This may have profound consequences for river ecosystems (Bellard et al., 2012), for example influencing the recruitment, growth and survival of Atlantic salmon and brown trout (Jonsson and Jonsson, 2009), or changing the abundance and species composition of benthic macroinvertebrates (Durance and Ormerod, 2007).

This paper reports over 20 years of annual benthic algae surveys from two pristine boreal stream sites in the Rondane area, which is Norway's oldest national park and probably one of the least impacted catchments that today exist in Europe. Species specific surveys of benthic algae were coupled to continuous measurements of river discharge and climate data measured in close vicinity to the benthic algae sites. The aims were to report natural variation in benthic

algal cover and diversity, i.e. variation at sites that are subject to as little anthropogenic impact as can reasonably be expected in Europe and to study whether year-to-year variation in benthic algal assemblages and cover was related to hydrological regime or climate parameters. The following hypotheses were tested: (1) high algal cover occurs after large spring floods; such a phenomenon was observed by Power et al. (2008) and may occur when the negative scouring effect of floods on benthic algae is overcompensated by the positive effect of grazer removal; (2) temperature effects on benthic algal assemblages and biodiversity are stronger than those of hydrological regime. This would occur because increased temperature could have an additive effect on algal growth by directly stimulating photosynthesis and by reducing springtime abundance of benthic invertebrates, including grazers (via an altered emergence phenology, increased predation by fish, as well as increased loss rates of litter to decomposition; Durance and Ormerod, 2007). In contrast, spates may have an antagonistic effect by reducing algal biomass, but at the same time also removing grazers, which in turn favors algal biomass development.

2. Material and Methods

2.1 Study area

The Atna river basin is located in the northeastern part of Southern Norway, and drains a catchment area of 1318 km². The river has a total length of 97 km between the source at >2000 m above sea level (a.s.l.) and the confluence with the river Glomma at 338 m a.s.l. (Tvede and Halvorsen, 2004). About half of the watershed is situated above the upper tree-line (between 1000 and 1150 m a.s.l.). The uppermost reaches lie within the Rondane national park, which was established in 1962 and is Norway's oldest national park. There are no glaciers in the Rondane mountains, but a few permanent snowfields persist in some of the highest areas. The climate in the Atna area is continental, with little precipitation and relatively cold winters (Hesthagen and Sandlund, 2004).

In the area north and northwest of Lake Atnasjøen, where the samples were taken, nutrient-poor sparagmite (a feldspar-sandstone), moraine and glacifluvial materials are covered by lichen- and heath-dominated vegetation with low productivity (Tvede and Halvorsen, 2004). River discharge is not regulated, and human settlement in the upper river basin, where the samples were taken, consists of very few scattered farms and cabins. The levels of acid components in the precipitation are and have been low, although the area did indeed receive some acid precipitation (Hesthagen and Sandlund, 2004). In September 2013, total-

phosphorus concentrations at the sites “Atna” and “Li” (Fig. 1) were 3 and 5 $\mu\text{g l}^{-1}$, respectively (unpublished data). Calcium concentrations at the sampling sites are generally below 1 mg l^{-1} , and conductivity is usually well below 10 $\mu\text{S cm}^{-1}$ (unpublished data). The Atna catchment thus provides a benchmark where human interference is practically limited to climate change. This allows the analysis of natural variation and long-term trends, without a confounding impact of common pressures such as eutrophication.

2.2 Dataset

Benthic algae

Samples of benthic algae were taken at two sites: “Atna” (latitude 61.852, longitude 10.226, elevation 701 m, river width ~ 40 m), and “Li” (latitude 62.007, longitude 10.013, elevation 740m, river width ~ 12 m; Fig. 1). While Atna is the outlet of a large oligotrophic lake (Lake Atnasjø, surface area 5 km^2 , max. depth 80 m, mean depth 35 m; Tvede and Halvorsen, 2004), Li is a headwater stream situated about 15 km upstream Lake Atnasjø, with no major lakes further upstream. The sediment at both sites is dominated by cobbles (6-20 cm), with boulders, gravel and occasionally some sand in between. Both sites experience only little shading from adjacent vegetation. Soft-bodied benthic algae (= algae including cyanobacteria attached to the river bottom or in close contact on or within patches of attached aquatic plants, but excluding diatoms) were sampled once in 1989 at Atna, after which annual sampling commenced in 1994. At Li, samples have been taken yearly since 1988 with the exception of 1993, when no benthic algae were collected. Each year samples were taken in late summer/early autumn (between August 15 and September 27). During this period, algal cover usually is at its maximum (long term experience at the Norwegian Institute for Water Research).

Samples were taken according to European standard procedures (EN 15708:2009) along an approximately 10-m length of river bottom using an aquascope (i.e. a bucket with a transparent bottom). At each site, percent cover of each form of macroscopically visible benthic algae was recorded, and samples were collected and stored separately in vials for species determination. In addition, microscopic algae were collected from ten cobbles with diameters ranging between approximately 10 and 20 cm, taken from each site. An area of about 8 x 8 cm from the upper side of each stone was brushed with a toothbrush to transfer the algae into a beaker containing approximately 1 L of river water from which a subsample was taken. All samples were preserved with a few drops of formaldehyde to a final concentration

of approximately 0.5%. The preserved benthic algae samples were later examined under a microscope (200 to 600 × magnification) and all non-diatom algae identified to species, wherever possible. For some genera of filamentous green algae whose vegetative forms cannot be determined to species level (e.g. *Spirogyra* Link or *Mougeotia* C. Agardh) categories based mainly on filament width were used (see Schneider and Lindstrøm (2009; 2011) for further details). The primary identification keys used were Geitler (1932), Komarek and Anagnostidis (2007), Gutowski and Förster (2009), and John et al. (2011) as well as their respective earlier editions. Abundance of each microscopic taxon was estimated in the laboratory as “rare”, “common” and “abundant”. These estimates were later translated into percent cover as 0.001, 0.01 and 0.1%, respectively. Macroscopic algae whose percent cover was noted as “<1%” in the field, were noted as “0.1%” in the database. For all other taxa, the percent cover that was estimated in the field was used. Samples were taken and analyzed by few people only, who worked in close collaboration with each other, to ensure taxonomic congruence during the study. Unfortunately, no data exist for benthic diatoms. Field and microscopic observations suggest, however, that diatoms were rare at both sites, and neither cover nor species richness is expected to reach values that would influence the general pattern of benthic algal assemblages.

Hydrology

Hydrological data have been recorded by the Norwegian Water Resources and Energy Directorate (NVE) throughout the study period, and were stored in the HYDRA II database. The NVE gauging stations are situated less than 1 km from the sites for benthic algae collection, respectively (site Atna: NVE number 2.32, latitude 61.8519, longitude 10.2221, elevation 701 m; site Li: NVE number 2.479, latitude 62.0010, longitude 10.0003, elevation 758 m). No tributaries occur between the gauging stations and the respective sites for benthic algae collection. At each site, discharge (in $\text{m}^3 \text{s}^{-1}$) was measured by a datalogger that now is in direct communication to NVE in Oslo. Discharge measurements at Atna commenced in 1917 (Tvede, 2004), while continuous discharge measurements from Li only are available from May 1997 (with sporadic earlier measurements starting in April 1988). For each site, available discharge data from 1980 to 2013 were extracted from the HYDRA II database as daily averaged values.

At Li, concentration of suspended mineral and organic particles (in mg/l) have been measured by NVE each year between the end of April and the beginning of October since 1988 (with

the exception of 2009). These data were extracted from the HYDRA II database as daily averaged values. No data exist for suspended particles at Atna, but concentrations at this site are expected to be practically zero, since it is the outlet of Lake Atnasjø. This lake is almost 9 km long and has a theoretical retention time of 6 months, which means that it acts as an efficient sediment trap (Halvorsen, 2004).

Climate

Monthly averaged climate data were extracted from the web portal of the Norwegian Meteorological Institute (eklima.met.no). Data on precipitation and snow depth were taken from Atnsjøen (site number 8720, latitude 61.8902, longitude 10.1398, elevation 749 m, situated 6.5 km NW of the benthic algae site Atna), and Atndalen-Eriksrud (site number 8770, latitude 61.9723, longitude 10.0268, elevation 731 m, situated 4 km south of the benthic algae site Li). For the sake of clarity, I hereafter refer to measurements from Atnsjøen as “Atna”, and those from Atndalen-Eriksrud as “Li”. The closest station with continuous records of temperature since 1988 is located in Venabu (site number 13420, latitude 61.6513, longitude 10.1082, elevation 930m), which is 24 km SSW of the benthic algae site Atna, and 40 km south of Li (Fig. 1). The temperature data from Venabu have been used as explanatory variables for both benthic algae sites.

As an estimate for long-term climatic variation, the Hurrell North Atlantic Oscillation (NAO) Index (principal components-based) was downloaded from <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based> (National Center for Atmospheric Research Staff (Eds); last modified 16 Apr 2014). The index is calculated from the difference in sea surface pressure between the Azores and Iceland, with positive values associated with mild, wet winters in NW Europe, and negative values with cold, dry winters (Hurrell and Van Loon, 1997).

2.2 Data treatment

Response parameters

To explore species composition and abundance of the benthic algal assemblages, an NMDS (non-metric multidimensional scaling) was computed on the square-root transformed data. NMDS was used because, in contrast to other ordination methods, it can also handle non-linear responses. The NMDS was computed using the metaMDS function in R version 2.14.2

(R Development Core Team, 2012), extended with the “vegan” package 2.0-4 (Oksanen et al., 2012). Bray-Curtis was used as dissimilarity measure because it is less dominated by single large differences than many other dissimilarity measures (Quinn and Keough, 2002). Prior to NMDS, “problematic” taxa, i.e. taxa that were determined to species level in some, but to genus level in other years, were merged to genus level (e.g. *Homoeothrix* sp., *Calothrix* sp., *Phormidium* sp.). In order to avoid the occurrence of a large number of filament width categories, where some only rarely occurred, *Mougeotia* and *Oedogonium* filament width categories were summarized into “narrow” (= filament diameter less than 12 µm for *Mougeotia*, and less than 20 µg for *Oedogonium*, respectively) and “broad”. After taxon merges, taxa which still had less than four occurrences during all years were removed, in order to avoid an influence of rare taxa on the overall benthic algal pattern.

In addition to NMDS scores, the following response parameters were calculated for each site and each year: 1) taxon richness (calculated from the original taxon list, i.e. prior to the taxon merges performed for the NMDS analysis); 2) total cover of benthic algae (calculated as sum of cover of all taxa); 3) cover of filamentous green algae and 4) cover of *Phormidium* sp., respectively, because they often are viewed as signs of ecological degradation (Hart et al., 2013); 5) the PIT-index (“Periphyton Index of Trophic status”; Schneider and Lindstrøm, 2011) was calculated based on benthic algal species composition, because it provides a link to eutrophication and ecological status assessment (PIT ranges from 2 to 69, where high values indicate that the algal assemblage is dominated by eutrophic taxa); 6) Bray-Curtis dissimilarity of benthic algal assemblages between consecutive sampling years, because it provides a measure of the stability of benthic algal assemblages. Other response parameters were considered (e.g. cover and number of cyanobacterial taxa having heterocysts, cover of red algae, etc.), but omitted from further analyses since these taxa only occurred in low abundances.

After exploratory analysis, data were log-transformed where necessary to improve normality and homoscedasticity (Table 1). Each response parameter was then checked for correlation with the Julian day of benthic algal sampling by using Pearson product-moment correlation (Bray-Curtis dissimilarity between years was checked against the difference in Julian sampling day between the same two years). In case of a significant correlation, the value of the response parameter was standardized to day 250 (i.e. September 8) by using linear regression (because visual inspection of the plots indicated no non-linear relationships). To illustrate time series data, generalized additive models (GAM) were computed using the *mgcv*

package in R (Wood, 2011), because this method is flexible and can show possible nonlinear relationships.

Explanatory parameters

Richter et al. (1996) defined several “indicators of hydrologic alteration” to statistically characterize hydrological variation within a year. They are categorized into the following five groups, which are considered useful to quantitatively evaluate the impact of hydrological regime on aquatic biota: 1) mean discharge values, 2) magnitude of annual extremes, 3) timing of annual extremes, 4) frequency and duration of high and low pulses, and 5) rate of change. I calculated 31 variables from the daily averaged discharge values, which were assigned to these five categories (Table 2). In addition, the base flow index (= the ratio of base flow to total stream flow) was calculated using the “lfstat” package in R (Koffler, 2013).

Altogether, 58 explanatory variables were compiled for the site Atna, and 64 for Li (local climate parameters, NAO, hydrology, and water particle concentrations which were measured only at Li; Table 2). After visual inspection of the data, only water particle concentrations were log-transformed to improve normality and homoscedasticity, while the remaining parameters were used untransformed. In order to allow for lagged responses of benthic algae, each explanatory variable was included two times in the dataset: a) each response variable was related to the explanatory variable during the 12 months preceding benthic algal sampling, and b) with an additional time lag of one year (i.e. each response variable was related to the explanatory variable during the penultimate year before sampling). Data analysis was started by inspecting scatter plots of each explanatory variable against each response variable, in order to check for possible non-monotonous (e.g. hump-shaped) relationships. None of the $2 \times 8 \times 58 = 928$ plots at Atna, and $2 \times 8 \times 64 = 1024$ plots at Li indicated a non-monotonous relationship.

Multivariate data analysis followed two different approaches: 1) reduction of the many explanatory variables to a small number of derived variables that summarize the original information; PCA (principal component analysis) was used on the scaled data because it is most effective as a variable reduction procedure when there are linear relationships between variables (Quinn and Keough, 2002); the PCA analysis focused on the year preceding benthic algae sampling; 2) linear models were computed that predicted each response variable from a set of explanatory variables for each site; for the modelling, both the lagged and the non-lagged variables were considered. In order to avoid overfitting and autocorrelation among the

explanatory variables, an iterative process was applied to reduce the number of explanatory variables. i) Pearson correlations between each response and each explanatory variable (including the time-lagged variables) were performed; ii) for each response variable and each site, all explanatory variables that were significantly correlated with the response variable were selected; iii) Pearson correlations among those explanatory variables that were significantly correlated with the response variable were performed, separately for each response variable and each site. Strongly autocorrelated explanatory variables (Pearson $r > 0.5$) were grouped, and from each group only the variable having the highest Pearson r with the response variable was kept. Then, for each response variable and each site, a linear model was computed using the MASS-package in R (Venables and Ripley, 2002), with explanatory variables selected through forward selection based on AIC (Akaike information criterion). Lastly, for each response variable and each site, an ANOVA on the selected model was performed, and the model was refitted using exclusively significant explanatory variables. This stepwise process ensured that only a minimum number of explanatory variables were entered into the final models, i.e. the models are conservative and no overfitting occurred. I did so because the aim was not to model the response parameters as exactly as possible in the existing dataset, but to find those environmental variables that were related significantly and meaningfully to the response variables, such that they also may be useful for predicting future changes. The process also resulted in the removal of strongly autocorrelated explanatory variables, since from each group of autocorrelated variables only one was entered into the model. For each model, however, all correlated explanatory variables are mentioned in the Appendix, and model results were interpreted accordingly.

Due to equipment malfunctions, some data were missing for some explanatory variables in some years. I decided against estimating missing values from the existing dataset, because I expected extreme events to impact benthic algal assemblages, and data logger breakdowns may well be caused by extreme events. Estimating missing values could thus introduce bias to the data.

3. Results

3.1 Variation in climate, hydrology and benthic algal assemblages

The climate was continental, with a precipitation maximum during summer. Average annual precipitation during the study period was 517 mm at Atna, and 600 mm at Li (Table 2).

Average discharge was 10 m³/sec at Atna, and around 3.5 m³/sec at Li. Mean air temperature

was above zero between May and October. Summary statistics for the environmental data are given in Table 2. Both sites exhibited gradual changes in benthic algal assemblages (along NMDS axis 1). While total cover of benthic algae tended to increase during the study period at Atna, no trend was observed at Li. In contrast, the eutrophication index PIT increased slightly at Li, but not at Atna. In accordance with general climate change observations (IPCC 2013), summer temperatures increased during the study period. The general climatic trend towards a decrease in spring snow cover and an increase in frequency and intensity of heavy precipitation events (IPCC, 2013) was reflected at Li, but not at Atna. This is plausible because the relief of the Rondane mountains can lead to considerable local differences in climate despite the relative proximity of the sites.

At both sites the hydrograph recorded regular winter minima followed by spring floods caused by snow melt (Fig. 2). While two extreme floods occurred at Atna in 1995 and 2013, Li exhibited additional peaks in 1988, 1989, 2003 and 2011 (there also was a major flood in 1995 at Li; however, the gauging station did not operate). With the exception of 2003, when the peak occurred in the middle of August, all these annual peaks were associated with spring floods. Total algal cover varied from 6 to 100% at Atna, and from 3 to 50% at Li (Table 2). Both sites exhibited a maximum in benthic algal cover after 2005, but total cover peaked slightly earlier at Li, and this peak was narrower than at Atna (Fig. 3). GAM models for the remaining response variables (Fig. S1) indicate that the peak in total algal cover at Atna was mainly caused by filamentous green algae, while the filamentous cyanobacterium *Phormidium* sp. contributed most to total algal cover at Li. Except a general trend towards an increasing PIT index at Li, no further trends or patterns were observed in the response variables (Fig. S1).

3.2 Effect of spring floods on algal cover and assemblages

There was no relationship between maximum spring discharge and benthic algal cover for the years when spring floods were lower than 10 times the average discharge (Fig. 4). In years where spring discharge exceeded 10 times the average discharge, total algal cover seemed constrained to $\leq 20\%$ at Atna, and $\leq 10\%$ at Li (Fig. 4). There are, however, too few observations with high spring maximum discharge, such that Chi-square tests for the groups “higher versus lower than 10 times average discharge” and “more versus less than 20% cover” (10% cover for Li) were not significant, although Li was almost so ($p=0.058$).

However, hypothesis 1, that large algal cover occurs after large spring floods, was not supported. If any it is the opposite.

The two extreme floods at Atna in 1995 and 2013 did not lead to any major changes in benthic algal assemblage (Fig. 5; inspect the length and direction of the line between the year in which the flood occurred, and the preceding year). In contrast, at Li all extreme spring floods in 1989, 1995, 2011 and 2013 caused a shift towards lower values on NMDS axis 1, and – to a less extent – towards higher values on NMDS axis 2 (Fig. 5). This corresponds to a lower abundance of the cyanobacteria *Phormidium* sp. and *Schizothrix* sp., as well as the filamentous green alga *Microspora amoena* along NMDS axis 1, and lower abundances of the green algae *Penium* sp., *Spirogyra* sp., *Gongrosira* sp. and *Microspora palustris* var. *minor* along NMDS axis 2 (Fig. S2). The late flood in August 2003 had the opposite effect (the effect of the large spring flood in 1988 could not be evaluated since this was the first year benthic algae were sampled at Li).

3.3 Influence of climate and hydrological regime on benthic algal cover and assemblages

The first principal component (PC1, i.e. the most important summarized gradient in the environmental variables) explained 21% and 28 % of total variation in the environmental variables of the year preceding benthic algal sampling at Atna and Li, respectively (Table S1). At Atna, PC1 was related to median and minimum annual discharge, mean winter discharge, as well as the base flow index (BFI). High median and minimum annual and winter discharge and high BFI scores (corresponding to a hydrological regime that is dominated by base flow, not by run-off) correlated with high cover of filamentous green algae, and high total cover of benthic algae (Table S1). In contrast, PC1 at Li was related to the magnitude of annual extreme flows, the rates of changes in flow, maximum particle concentrations, and the base flow index (Table S1). NMDS 2 scores (i.e. a measure of species assemblages) and total cover of benthic algae were related to PC1 at Li. High maximum discharge and particle concentrations, and a low BFI (i.e. a hydrological regime dominated by run-off) corresponded to a low cover of benthic algae, and lower abundances of the green algae *Penium* sp., *Spirogyra* sp., *Gongrosira* sp. and *Microspora palustris* var. *minor* (along NMDS 2) (Table S1). No other principal component correlated with any of the response variables.

Complete results including model parameters for each site-specific linear model computed from measured explanatory variables are given in Tables S2 a and b. Table 3 summarizes these results. Generally, the models explained more of the variance at Li than at Atna (Table

3). Taxon richness (often interpreted as a straightforward measure of biodiversity) was generally poorly predicted suggesting that climate and hydrological regime had no major effect on benthic algal diversity at the sampling sites. High temperatures tended to increase benthic algal cover at both sites, and April temperature was particularly important at Atna (the logarithm of total cover increased by 0.1 for each degree in average April temperature; Table S2 a). Reduction of benthic algal cover was caused by low minimum discharges at Atna (possibly caused by drying and freezing of parts of the river bed), while high particle concentrations (generally associated with spates) reduced benthic algal cover at Li, likely due to their scouring effect. A surprising finding was that negative values for summer NAO, associated with cool, cloudy summers in Northwestern Europe (Folland et al., 2009), increased cover of filamentous green algae at Atna. The same tendency was seen for the total cover of benthic algae at this site, only the influence of summer NAO was overridden by the effects of April temperature and minimum discharge (while it was the other way round for the cover of filamentous green algae, i.e. the effect of April temperature and minimum discharge was overridden by the influence of summer NAO). The cover of the cyanobacterium *Phormidium* sp. increased with increasing annual temperatures (which were associated with less snow), and decreased with prolonged periods of high discharge events, possibly due to movement of the stream bed. While the stability of benthic algal assemblages, expressed as Bray-Curtis dissimilarity between consecutive years, was unrelated to any of the measured environmental variables at Atna, high mean and maximum discharge, as well as high mean and maximum particle concentrations caused unstable benthic algal assemblages at Li. While high annual temperatures (correlated with high August temperatures) were associated with an increase in the periphyton index of trophic state PIT at Atna, PIT at Li was increased by late floods, low winter discharge and high annual precipitation.

While flood-related variables by and large had an effect within the year they occurred, temperature-related explanatory variables were in some instances most influential in their time-lagged, but in other instances in their non-lagged form (Table S2 a and b). This may indicate that temperature affects benthic algae via growth and competition, which may have longer-lasting consequences for benthic algal assemblages. In contrast, floods have an immediate destructive effect. Models for total cover of benthic algae, as well as for cover of filamentous green algae at Li included both the non-lagged and the lagged particle concentrations (Table S2 b). This suggests that consecutive years of high floods carrying high particle concentrations had an additive effect.

The relative influence of temperature versus hydrological regime differed between the two sampling sites. At Li, total algal cover, cover of filamentous green algae, the PIT index and Bray-Curtis dissimilarity between consecutive years were mainly related to hydrological parameters (Table 3 and Table S2 b), and none of the response variables whose models had an $R^2 > 0.35$ was related to temperature only. At Atna, all response variables whose models had an $R^2 > 0.35$ (total algal cover, cover of filamentous green algae, PIT index; Table 3, Table S2 a) included both temperature-related and hydrology-related explanatory variables, but temperature-related variables in each case explained more of the variance than hydrology-related variables (Table S2 a; sum of squares for the variables included in the models for total algal cover, cover of filamentous green algae, and PIT). These findings thus do not generally support hypothesis 2, which assumed that temperature effects on benthic algae would be stronger than the effects of hydrological regime. Instead, the relative importance of temperature versus hydrological regime seemed to depend on river type; temperature was more important for the lake outlet Atna, while hydrology was more important for the headwater stream Li.

Averaging and summarizing explanatory variables into principal components led to similar overall results for Li (the magnitude of annual extreme discharges. i.e. hydrology-related variables, were related to benthic algal assemblage and total cover), but underestimated the influence of temperature-related variables at Atna (temperature and climate related variables were related to PC2, which had no significant correlation with any of the response variables although correlations with PIT and total algal cover were close to being significant; Table S1).

4. Discussion

4.1 Explaining the past

Both sites, the lake outlet Atna and the headwater stream Li, have experienced as little confounding impact by human activities as today can reasonably be expected in Europe. Nevertheless, cover of filamentous green algae during the study period reached 100% at Atna, and of the filamentous cyanobacterium *Phormidium* sp. 50% at Li (Table 2). Both have been suggested to be indicative of degradation (Hart et al., 2013). In contrast, the data presented here suggest that they may also be abundant in catchments that do not experience direct anthropogenic degradation.

To my knowledge, there is only one study that analyzed the effects of peak discharge on benthic algal development in streams based on long-term data series. Power et al. (2008) observed that blooms of a filamentous green alga in the Eel river in California were larger if floods during the preceding winter exceeded “bankfull discharge”, an estimated value they considered sufficient to mobilize much of the river bed. They explained this effect by the removal of predator-resistant grazers by flood scour. These results match well with grazer exclusion experiments performed in a eutrophic stream in Ireland that showed that the absence of grazers quickly leads to the development of high biomasses of benthic algae (Sturt et al., 2011). In contrast, benthic algae at Atna and Li showed no signs of increased cover in the year following a high flood. Instead, floods below 10 times the average discharge had no impact on benthic algal cover, while floods exceeding that value seemed to constrain benthic algal cover (Fig. 4.). This appears at odds with the results of Power et al. (2008), even if the effect at Atna and Li was not significant due to the low number of extreme floods. Two possible explanations may apply: i) even the most extreme floods at Atna and Li were not sufficient to remove grazers, while they indeed reduced benthic algal cover directly by scouring; ii) benthic algal cover was controlled by bottom-up processes at Atna and Li, but by top-down processes in the streams studied by Power et al. (2008) and Sturt et al. (2011); removal of grazers at top-down controlled sites may lead to an increase in benthic algal biomass within few weeks (Sturt et al. 2011), while slow growth of benthic algae at the extremely nutrient-poor sites Atna and Li may make the effect of a scouring flood persistent for a period of several months. There are insufficient data on macroinvertebrates from Atna and Li that would allow these possible explanations to be tested. However, studies that analyzed flood effects on both macroinvertebrates and periphyton reported that either both were affected (Danehy et al., 2012; Fuller et al., 2011; Robinson and Uehlinger, 2008), or neither of the two was affected (Tonkin and Death, 2014), or that macroinvertebrates were more sensitive than periphyton (Robinson, 2012). This rather undermines the possibility that floods did remove algae but not grazers. It thus lends indirect support to the hypothesis that large floods, after a period of few weeks, tend to increase algal cover in top-down controlled streams, while the negative impact of flood scouring may persist for several months (from the spring flood to the sampling in autumn) in nutrient-poor streams.

Generally, climate and hydrology explained more of the variation in benthic algal assemblages and cover at Li than at Atna (Table 3). This can be interpreted as follows; i) aquatic bryophytes compete with benthic algae for nutrients; since aquatic bryophytes are not

abundant at Li, but may reach up to 50% cover at Atna (personal observations; no other macrophytes occur) they may have blurred nutrient-mediated effects of climate and hydrology at Atna, but less at Li; ii) Atna is the outlet of a large lake, which may be expected to buffer effects of air temperature and precipitation, while the headwater stream Li is more directly affected by climate and experiences faster changes in stream discharge. This also explains why large floods were associated with unstable benthic algal assemblages at Li, as expressed by Bray-Curtis dissimilarity among consecutive years, while stability of benthic algal assemblages at Atna was poorly related to variability in climate and hydrology (Table 3).

My second hypothesis, which stated that benthic algae are more affected by temperature than by hydrological regime, was not generally supported. While temperature indeed was most important for the lake outlet Atna, hydrology explained most of the variation in the headwater stream Li (Tables 3 and S2). This may again be explained by the buffering capacity of Lake Atnasjø, which accumulates more heat during summer, while Li experiences faster changes in discharge and more extreme events.

Climate and hydrology were related to benthic algal species assemblages (NMDS scores), although not particularly strongly (Table 3). Specifically, long periods of high discharge events reduced the cover of the filamentous cyanobacterium *Phormidium* sp. (Table 3). Since this genus not only tolerates but often even dominates at high flow velocities (Hart et al., 2013), its reduction at prolonged periods of high discharge is not readily explained by flow velocity alone, but by substrate movement and abrasion by particles that are associated with high discharge.

Hydrology had no effect on benthic algal taxon richness (Table 3). This may suggest that sufficient relicts of algal populations remain after flood scouring to permit rapid recolonization. These results are in line with observations by Biggs and Smith (2002), who did not detect general effects of flood disturbances on benthic algal richness patterns in streams (although benthic algal richness often declined immediately after floods). Increased June temperatures tended to decrease taxon richness at Atna, while increased December temperatures tended to increase richness at Li (Table 3). Although it is tempting to explain this by increased stress of cold-water adapted species in a Nordic environment during warm summers (Brodie et al., 2014), as well as less freezing damages in warm winters, the effect was weak and must not be overinterpreted. However, Piggott et al. (2015) also observed a decrease in periphyton taxon richness with increasing temperature in enclosures without added sediment. This can be taken as support of the results at Atna and Li.

At both Atna and Li, increased temperatures tended to increase total benthic algal cover (Table 3). This effect may be caused by a directly enhanced growth of algae at higher temperatures, but also indirectly because warmer temperatures favor growth of the dominant fish species in the Atna river, brown trout (*Salmo trutta*) and Siberian sculpin (*Cottus poecilopus*; Hesthagen et al., 2004a). Both species mainly feed on benthic macroinvertebrates (Hesthagen et al., 2004b), so may remove more grazers at higher temperatures. Another indirect effect may be induced if increased decomposition of terrestrial organic matter at higher temperatures (Hayes et al., 2011) should lead to a concomitant increase of nutrient input into the streams. At Atna, April temperatures were particularly important (Table S2 a). In April, average air temperatures change from below to above zero (Table 2). Warm April temperatures may lead to an earlier start of the vegetation period, which may eventually lead to a higher biomass accrual of benthic algae. The effect of temperature was less pronounced at Li than at Atna, possibly because temperature effects at Li were overridden by the effect of scouring floods, which reduced benthic algal cover. The data from Atna and Li do not support results obtained by Davis et al. (2013), who found that biofilm ash-free dry mass in an oligotrophic north-American river was best explained by the number of days between peak flow and sampling. This is likely because Davis et al. (2013) sampled less than 80 days after peak flow, i.e. during a period when benthic algae may be expected to re-grow after scouring, while our samples were generally taken later (Table 2).

Biomass of filamentous green algae has been shown to decrease with increasing flow velocities (Biggs et al., 1998; Hart et al., 2013). The data presented here support this observation at Li, where high floods (via high particle concentrations) indeed reduced the cover of filamentous green algae (Table 3), likely by abrasion and movement of the stream bed. At Atna, however, there was no such relationship. Instead, high cover of filamentous green algae was mainly related to negative values for summer NAO, which are associated with cool, cloudy summers in Northwestern Europe (Folland et al., 2009). This result seems counter-intuitive, but may possibly be explained by the fact that in Lake Atnasjø, wind generated currents and internal seiches force deep water (from about 10 m depth) up to the surface at the outlet, such that the outflow becomes a mixture of surface and deep water (Halvorsen, 2004). If we accept that cool, cloudy summers also may be associated with a different pattern in wind intensity and/or direction compared to warm, sunny summers, then a higher contribution of deep water in the outlet of Lake Atnasjø may cause increased growth of

benthic algae via increased concentrations of bioavailable nutrients in deep compared to surface water.

4.2 Predicting the future

Climate change scenarios imply an increase in temperature, decrease in spring snow cover, increase in frequency and intensity of heavy precipitation, earlier spring floods, a decrease in magnitude of low flows as well as an increase in magnitude of high flows in the Northern Hemisphere (IPCC, 2013; Minville et al., 2008; Fowler and Kilsby, 2007). If this is valid also for Atna and Li, then we may expect the following future developments:

At Atna, climate change would lead to an increase in total algal cover via increased temperature, and to an increase in the PIT index via increased temperature and more sudden changes in discharge. At Li, climate change would lead to a change in benthic algal species assemblages via temperature, snow depth and maximum particle concentrations (related to the magnitude of floods). It would lead to a decrease of filamentous green algae due to higher particle concentrations associated with higher peak flows, and to an increase of *Phormidium* sp. due to the occurrence of less snow (and increased temperature). Climate change will have an ambivalent effect on total benthic algal cover at Li, because higher particle concentrations caused by higher peak floods will cause a decrease in algal cover, while less snow (higher temperatures) will lead to an increase. Likewise, the effect of foreseen climate change on the PIT index is ambivalent, since the foreseen earlier floods would decrease the PIT index, while more precipitation would increase it.

In summary, effects of climate change are likely to differ between Atna and Li. While Atna will become “greener” and slightly more eutrophic, Li will become more “bluegreen” (more *Phormidium* but less filamentous green algae). It seems plausible that these differences are related to Atna and Li being different stream types (lake outlet and headwater stream). Since both filamentous green algae and *Phormidium* sp. are quite common elements of the benthic algal flora in streams, it is also plausible to assume that the predicted effects of climate and hydrology on benthic algae at Atna and Li are representative of oligotrophic soft water lake outlets (Atna), as well as for small to middle-sized, oligotrophic, soft headwater streams (Li) in a boreal landscape.

In the present dataset, temperature was most important for explaining the cover and composition of algal assemblages at Atna, while hydrology explained most of the variation at

Li. Numerous factors, among them nutrients, light, temperature, and disturbance, interact to determine stream periphyton biomass and species composition (Pan et al., 1999; Bernhardt and Likens, 2004). This makes generalizations across different streams a bold undertaking. Nevertheless, it seems plausible that climate generally will affect lake outlets primarily via temperature, while headwater streams will primarily be affected via altered hydrology and particle concentrations.

Acknowledgements

The Norwegian Environment Agency is gratefully acknowledged for many years of funding the collection and analysis of benthic algae, the Norwegian Water Resources and Energy Directorate for providing data on hydrology and the Norwegian Meteorological Institute for data on local climate. I thank several colleagues at NIVA for collection and microscopic analysis of benthic algae over many years, several friends who spent part of their holidays for helping to keep up the time series in times of increasingly difficult funding, and Jan Vermaat and Martyn Kelly for critical comments on an earlier version of the manuscript. Data analysis was funded by the Research Council of Norway through the ECOREG-project (221398/E40) and NIVA's Strategic Institute Initiative "Climate effects from Mountains to Fjords" (208279).

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Table 1 Transformation of response parameters; data were log-transformed (log) when histograms indicated a skewed distribution, or standardized to Julian day 250 (stand_250) in case of a significant correlation between the response parameter (y) and the Julian day of sampling (x); for significant correlations, the equation, Pearson r and p are given; all other correlations between response parameter and Julian day of sampling were not significant.

	Atna	Li
scores NMDS1	stand_250 y = -0.023x + 5.72; r = -0.45, p = 0.04	-
scores NMDS2	-	stand_250 y = - 0.02x + 4.15; r = -0.5, p = 0.01
number of taxa	stand_250 y = 0.21x - 32.9; r = 0.54, p = 0.01	-
total algal cover	log	log
cover filamentous green	log	log
cover <i>Phormidium</i> sp.	log	log
PIT-index	-	stand_250 y = -0.03x + 13.5; r = - 0.56, p = 0.003
Bray-Curtis dissimilarity	-	-

Table 2 Summary statistics of response and explanatory variables at the sites Atna and Li; averages were taken for the years 1985 to 2013; see Methods for a description of variables were data series were shorter than 1985; “annual” refers to the 12 months preceding benthic algal sampling, that is from October to September; significant trends are indicated (Spearman rho for correlation with year; only correlations with $p < 0.05$ are indicated).

	Atna				spearman rho	Li				spearman rho
	mean	min	max			mean	min	max		
Response variables										
NMDS1 (Li: standardized to day 250)	0.042	-1.168	1.105	↑	0.65	0.000	-0.840	0.705	↑	0.64
NMDS2 (Atna: standardized to day 250)	0.000	-0.823	0.875			0.043	-0.549	0.668		
number of benthic algal taxa (Li: standardized to day 250)	19	11	26			15	7	21		
log (total cover of benthic algae)	1.41	0.79	2.01	↑	0.54	0.97	0.40	1.68		
log (cover filamentous green algae)	1.33	0.70	2.00	↑	0.64	0.50	0.01	1.20		
log (cover Phormidium)	0.05	0.00	0.48			0.47	0.00	1.49		
PIT-index (Atna: standardized to day 250)	5.28	4.36	6.49			5.99	5.08	7.27	↑	0.49
Bray-Curtis dissimilarity among consecutive years	0.52	0.11	0.84			0.53	0.12	0.88		
Hydrology										
<i>mean discharge values</i>										
monthly mean discharge October [m3/sec]	2.87	1.25	4.53			0.94	0.63	1.92		
monthly mean discharge November [m3/sec]	2.29	0.99	3.21			0.79	0.53	1.75	↑	0.49
monthly mean discharge December [m3/sec]	2.02	0.93	4.55			0.77	0.45	1.75		
monthly mean discharge January [m3/sec]	3.87	1.12	10.87			1.66	0.69	3.96		
monthly mean discharge February [m3/sec]	19.03	6.70	38.06			6.15	3.38	12.72		
monthly mean discharge March [m3/sec]	24.26	9.25	45.96			8.51	3.53	12.89		
monthly mean discharge April [m3/sec]	17.79	7.32	34.69			6.75	3.52	14.22		
monthly mean discharge May [m3/sec]	15.91	7.31	23.28			6.17	2.99	11.13		
monthly mean discharge June [m3/sec]	13.29	7.10	25.39			4.30	2.09	7.70		
monthly mean discharge July [m3/sec]	10.46	5.41	21.52			3.19	1.65	7.31		
monthly mean discharge August [m3/sec]	6.28	3.78	11.98	↑	0.36	1.85	1.05	4.21		
monthly mean discharge September [m3/sec]	4.07	2.32	7.46			1.25	0.73	2.26		
mean discharge October-September [m3/sec]	10.26	7.08	13.96			3.57	2.53	4.63	↑	0.62
median discharge October-September [m3/sec]	7.30	3.72	11.50			2.16	1.20	3.37		
0.25 percentile discharge October-September [m3/sec]	2.82	1.20	4.34			0.95	0.65	1.89		
0.75 percentile discharge October-September [m3/sec]	14.15	8.68	19.57			4.84	3.24	6.81	↑	0.61
<i>magnitude of annual extremes</i>										
one day maximum spring discharge [m3/sec]	63.72	30.23	158.63			30.48	10.66	90.00		
one day maximum discharge October-September [m3/sec]	66.35	36.87	158.63			29.45	10.66	54.74		
one day minimum discharge October-September [m3/sec]	1.77	0.88	2.51			0.69	0.41	1.65		
seven day maximum discharge October-September [m3/sec]	49.85	28.09	120.98			17.67	7.95	29.59		
seven day minimum discharge October-September [m3/sec]	1.79	0.89	2.53			0.69	0.42	1.66		
<i>timing of annual extremes</i>										
Julian day spring maximum (number)	152	123	175			157	121	191		
Julian day October-September maximum (number)	156	123	227			168	121	226		
days between sampling and spring maximum (number)	99	54	134			95	36	137		
<i>frequency and duration of high pulses (high pulse defined as > 0.75 percentile discharge)</i>										
number of high pulses October-September (number)	5	2	9			8	5	13		
average duration of high pulses October-September (number of days)	19	6	37			13	4	24	↑	0.53
days of high pulse October-September (number of days)	88	28	163			91	49	150	↑	0.63
<i>rate of change in flow</i>										
average rising limb October-September (number)	1.88	1.15	3.35	↓	-0.42	1.26	0.42	2.08		
maximum rising limb October-September (number)	23.41	10.55	58.44			16.27	4.34	36.36		
average falling limb October-September (number)	-0.94	-1.72	-0.61	↑	0.53	-0.67	-1.11	-0.29		
minimum falling limb October-September (number)	-13.92	-40.36	-4.12			-12.90	-26.45	-3.43		
base flow index (BFI)	0.73	0.61	0.81			0.68	0.54	0.84		
Local climate										
<i>temperature</i>										
mean temp. October [°C]	0.2	-3.8	3.2			0.2	-3.8	3.2		
mean temp. November [°C]	-4.5	-9.8	-0.9			-4.5	-9.8	-0.9		
mean temp. December [°C]	-7.7	-14.0	-2.4			-7.7	-14.0	-2.4		
mean temp. January [°C]	-8.0	-14.1	-3.7			-8.0	-14.1	-3.7		
mean temp. February [°C]	-8.3	-13.5	-2.9			-8.3	-13.5	-2.9		
mean temp. March [°C]	-5.7	-10.1	-0.8			-5.7	-10.1	-0.8		
mean temp. April [°C]	-1.2	-4.3	3.2			-1.2	-4.3	3.2		
mean temp. May [°C]	4.4	1.7	7.1			4.4	1.7	7.1		
mean temp. June [°C]	9.0	5.9	12.7	↑	0.42	9.0	5.9	12.7	↑	0.42
mean temp. July [°C]	11.5	9.5	14.8			11.5	9.5	14.8		
mean temp. August [°C]	9.9	7.2	14.5			9.9	7.2	14.5		
mean temp. September [°C]	5.3	2.4	8.7			5.3	2.4	8.7		
mean temp. October-September [°C]	0.4	-1.1	2.1			0.4	-1.1	2.1		
mean summer temp. (May-September) [°C]	8.0	6.1	10.0	↑	0.39	8.0	6.1	10.0	↑	0.39
heat sum (> 0°C) May-September (degree-days)	1234	945	1535	↑	0.38	1234	945	1535	↑	0.38
minimum winter temperature [°C]	-23.6	-32.7	-18.2			-23.6	-32.7	-18.2		
<i>precipitation</i>										
precipitation October-September [mm]	517	311	690			600	445	779	↑	0.50
summer precipitation (May-September) [mm]	334	138	541			363	243	569	↑	0.40
number of days with precipitation > 1mm during summer (May-September) (number of days)	50	23	77			53	35	90	↑	0.39
maximum snow depth [cm]	78	26	177			71	35	153	↓	-0.41
North Atlantic Oscillation (NAO)										
NAO (December-March) (number)	0.326	-2.550	2.510			0.326	-2.550	2.510		
NAO (December-February) (number)	0.274	-2.950	2.480			0.274	-2.950	2.480		
NAO (March-May) (number)	0.235	-1.640	2.360			0.235	-1.640	2.360		
NAO (July-August) (number)	0.040	-2.060	2.050			0.040	-2.060	2.050		
NAO (September-November) (number)	-0.023	-1.870	2.120			-0.023	-1.870	2.120		
NAO (annual) (number)	0.112	-3.620	2.500			0.112	-3.620	2.500		
Suspended particles (only at "Li")										
<i>mineral particles</i>										
log maximum [mg/l]						1.864	1.045	3.394		
log 95-percentile [mg/l]						1.151	0.425	3.062		
log average [mg/l]						0.663	-0.135	2.303		
<i>organic particles</i>										
log maximum [mg/l]						0.877	0.584	1.654		
log 95-percentile [mg/l]						0.482	0.218	1.209		
log average [mg/l]						0.167	-0.139	0.626		

Table 3 summary of the results from multivariate linear modelling; complete results are given in appendix (Tables S2 a and b);

explained variance: 😊 high ($R^2 > 0.6$), 😐 medium, ☹ low ($R^2 < 0.35$);

correlation between explanatory and response variable: ⬆ positive, ⬇ negative

Atna		Li	
assemblage (NMDS 1 and 2)	☹ $R^2=0.25$ and 0.27	minimum discharge general hydrologic regime (BFI)	😐 $R^2=0.43$ and 0.57
	<i>Zygnema</i> sp. and <i>Scytonematopsis starmachii</i> tended to dominate at high minimum discharge; broad <i>Mougeotia</i> sp. dominated at a hydrologic regime with a high contribution of run-off to total discharge, while the opposite was true for <i>Draparnaldia glomerata</i> ; effects occurred after a time lag of one year		high April temperatures led to an increased dominance of a.o. <i>Microspora amoena</i> and <i>Phormidium</i> sp.; mild, wet winters led to an increased dominance of a.o. <i>Spirogyra</i> sp. and <i>Microspora palustris</i> var. <i>minor</i> , while high particle concentrations (high floods) decreased the abundance of these species; effects of floods occurred in the same year, while climate effects occurred after a time lag of one year
taxon richness	☹ $R^2=0.21$	June temperature ⬇	☹ $R^2=0.29$
	the number of benthic algal taxa decreased slightly with increasing June air temperatures		warmer December temperatures slightly increased the number of taxa; effect occurred after a time lag of one year
total algal cover	😐 $R^2=0.44$	temperature (particularly April) ⬆ minimum discharge ⬆	😊 $R^2=0.74$
	warmer April temperatures (ice break of the lake upstream), and higher minimum discharge (less drying of stream bed) increased benthic algal cover		high concentrations of (organic) particles (associated with floods) and more snow (associated with lower annual temperatures) decreased algal cover; flood effects occurred in the same year, while snow (temperature) effects occurred after a time lag of one year
cover fil. green	😐 $R^2=0.46$	cool, cloudy summer ⬆ average August discharge ⬆	😐 $R^2=0.46$
	cool, cloudy, rainy summers (summer NAO) increased the cover of filamentous green algae		high concentrations of (organic) particles (associated with floods) decreased the cover of filamentous green algae
cover Phormidium	☹ $R^2=0.18$		😊 $R^2=0.70$
	<i>poorly predicted, too many zero values for meaningful modelling</i>		prolonged periods of high discharge decreased <i>Phormidium</i> cover (substrate movement), while less snow (high annual temperatures) increased <i>Phormidium</i> cover; effects occurred after a time lag of one year
PIT index	😐 $R^2=0.53$	temperature ⬆ sudden discharge changes ⬆	😊 $R^2=0.67$
	High (summer) temperatures and - to a less extent - sudden spates favored more eutrophic taxa (higher PIT)		late floods, low discharge (especially in January) and high precipitation led to more eutrophic algal assemblages; effect partly occurred with a time lag of one year
Bray-Curtis diss.	☹		😐 $R^2=0.59$
	<i>poorly predicted</i>		high average and maximum discharge (particle concentrations) caused unstable benthic algal assemblages

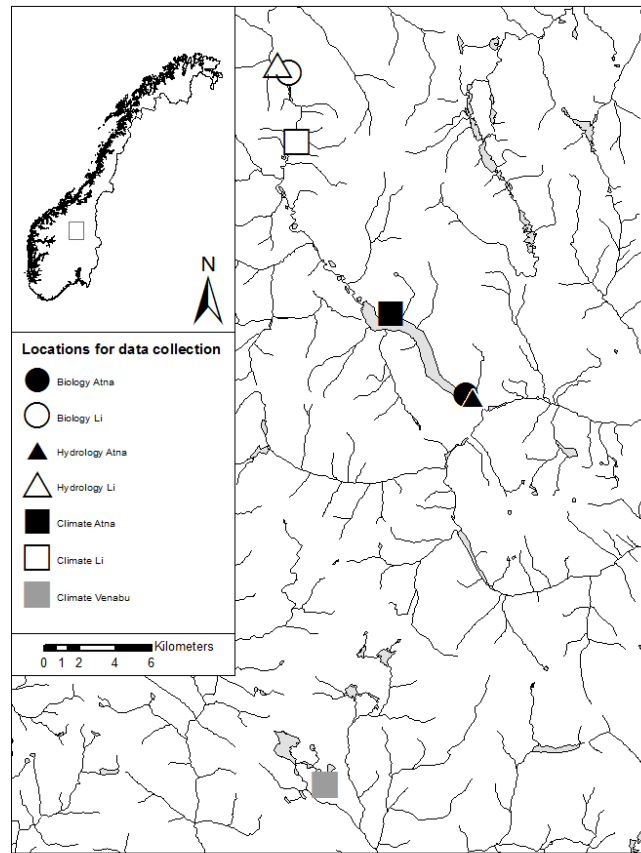


Fig. 1 Map showing the sites for collection of benthic algae (biology), hydrology and climate data in Norway. For the sake of clarity, all sites at lake Atnasjø are called “Atna”, and all sites close to Li are called “Li”.

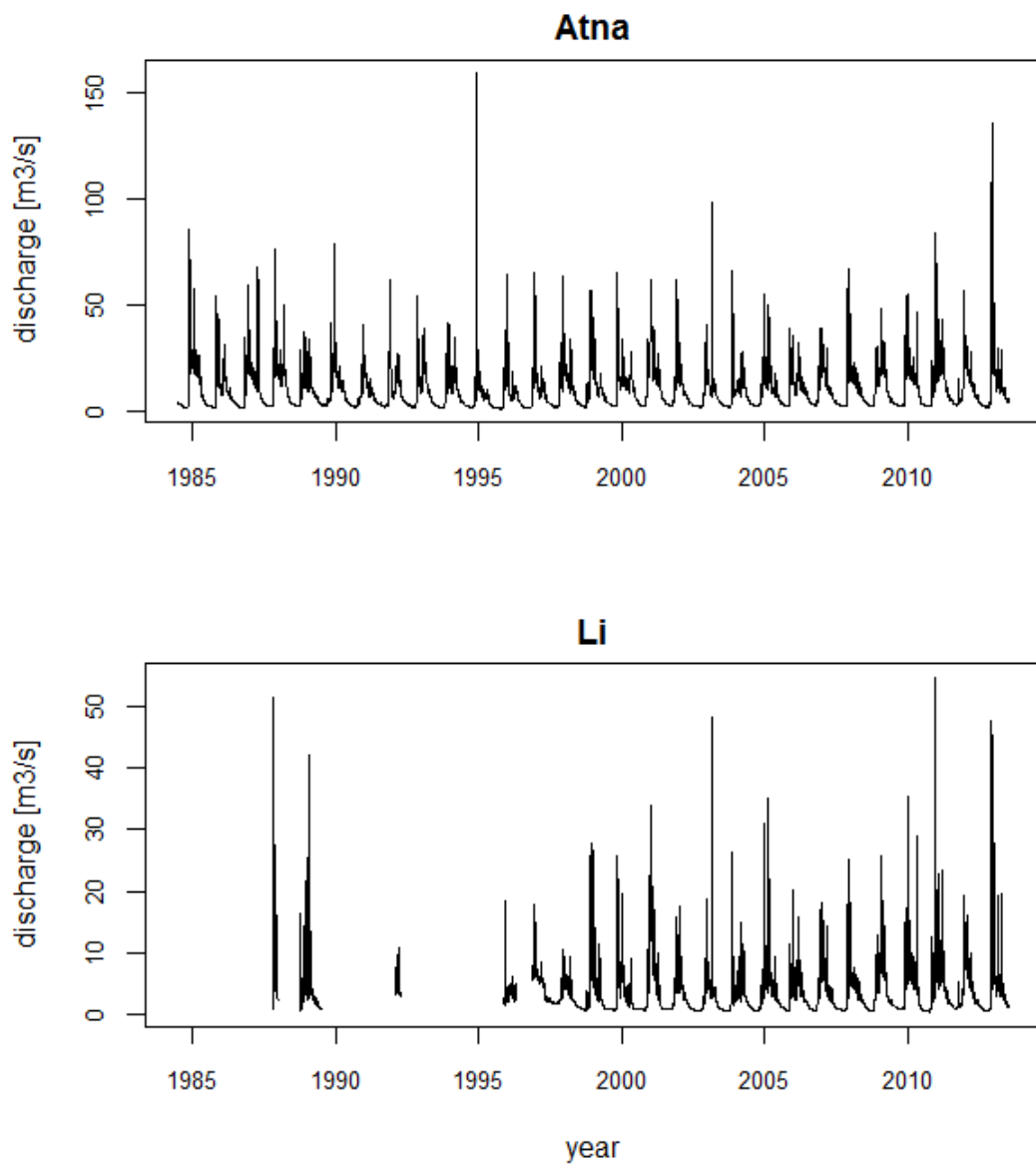


Fig. 2 Hydrograph for the sites Atna and Li, based on daily averaged values; note different scale of y-axes.

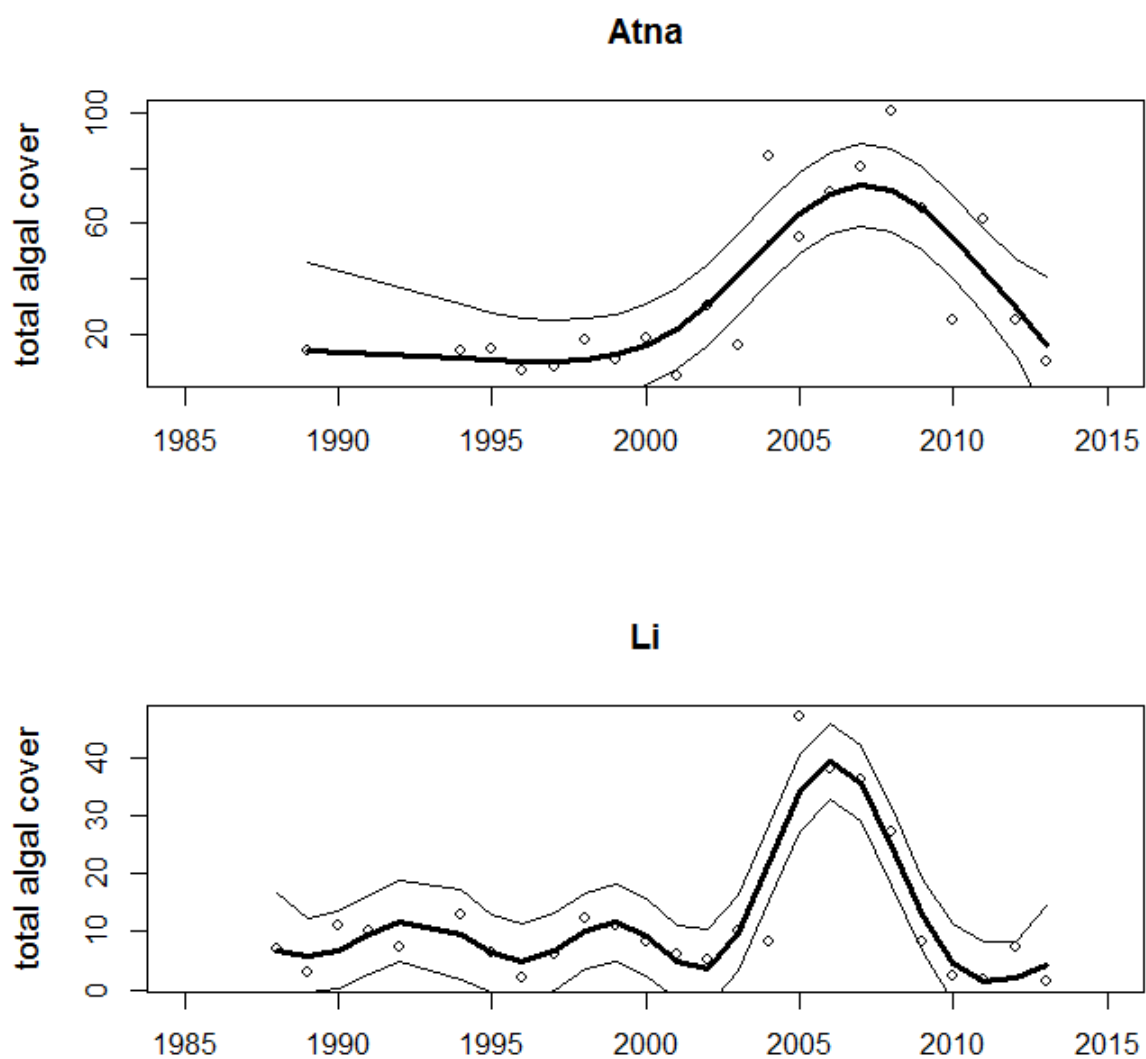


Fig. 3 GAM (generalized additive model; ± 2 SE) of autumn total algal cover at the sites Atna and Li; note different scale of y-axes.

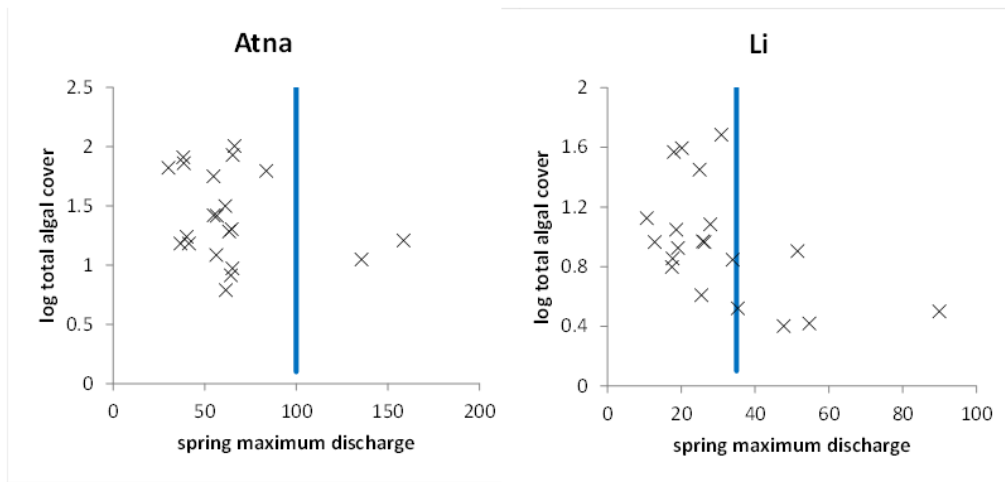


Fig. 4 Scatter plots of maximum spring discharge against total algal cover at the sites Atna and Li; vertical lines indicate 10 times average discharge; note different scale of x- and y-axes.

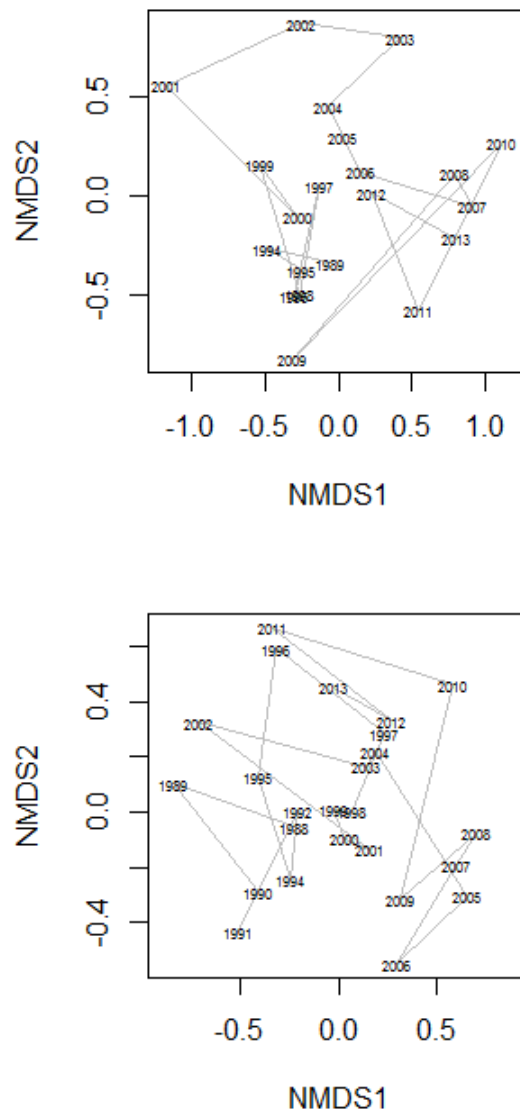


Fig. 5 Non-metric multidimensional scaling (NMDS) ordination plot of the benthic algal assemblages at Atna (top) and Li (bottom); site scores are scaled as described in Table 1; stress values are 0.17 for Atna, and 0.18 for Li; the markers lying on top of each other in the top panel are 1996 and 1998; plots for the species scores are provided in Fig. S2; extreme spring floods occurred at Atna in 1995 and 2013, while Li exhibited additional peaks in 1988, 1989, 2003 and 2011.

Supporting information

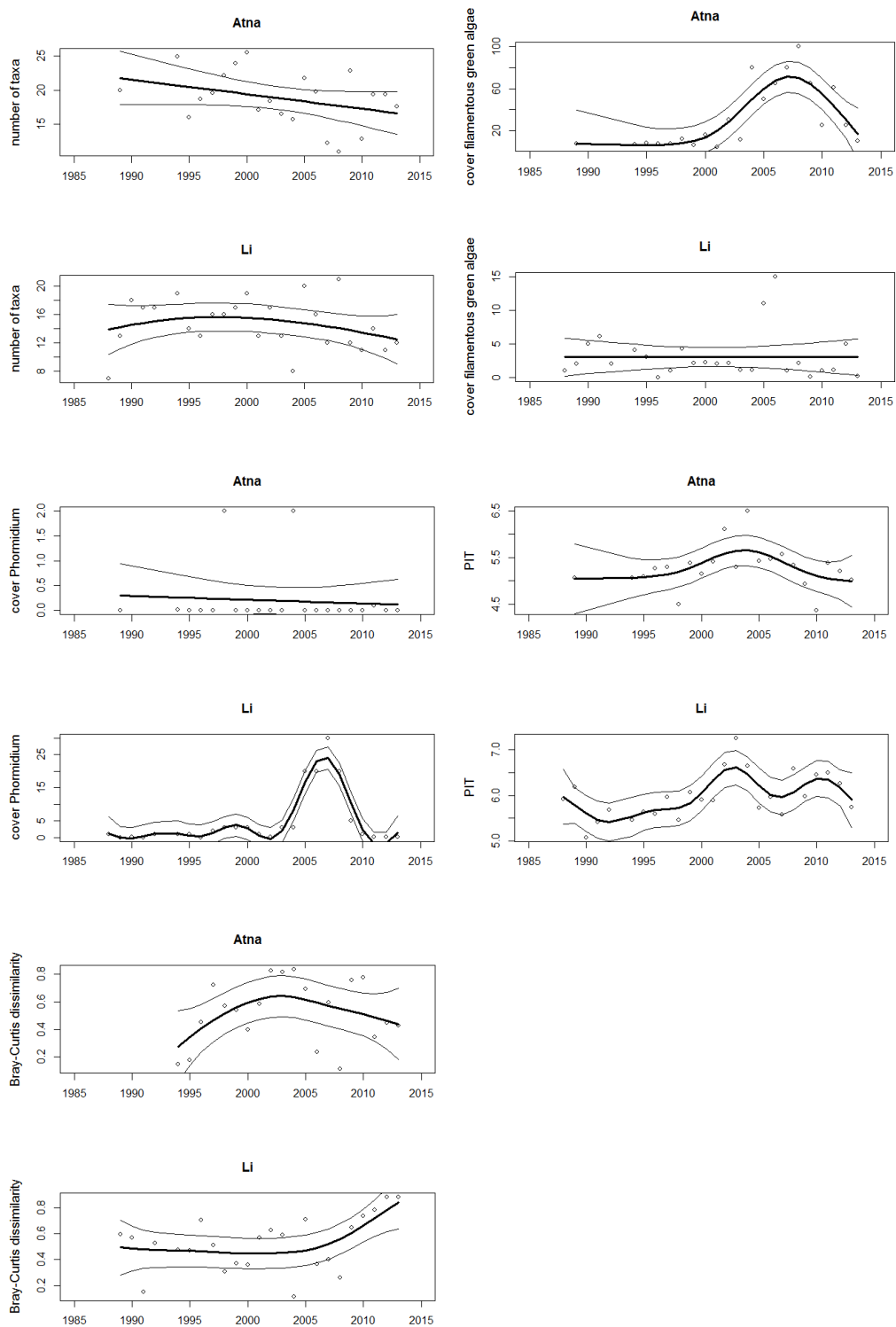


Fig. S1 GAM (generalized additive models; ± 2 SE) of response parameters at the sites Atna and Li; note different scales of y-axes

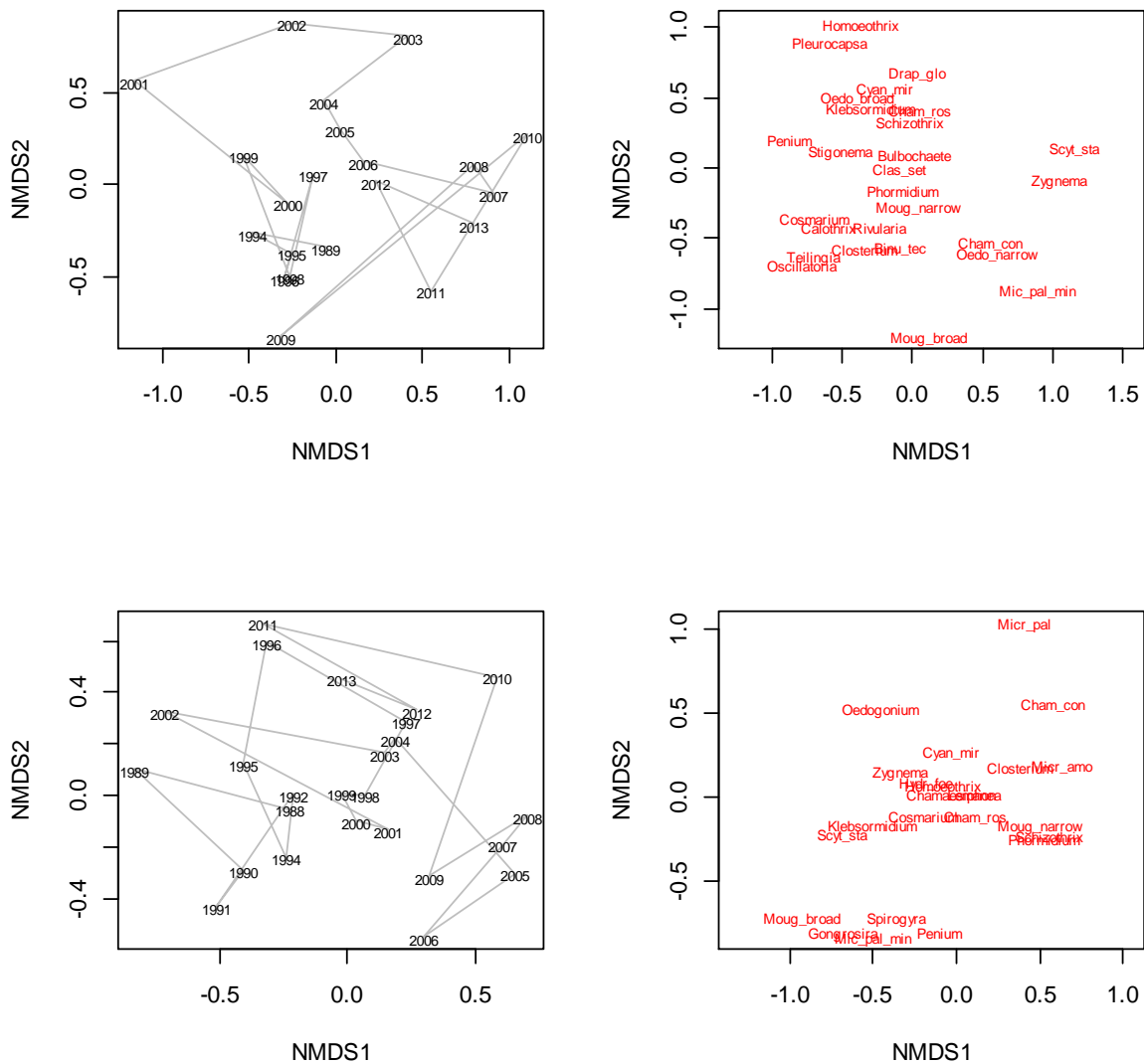


Fig. S2 Non-metric multidimensional scaling (NMDS) ordination plot of the benthic algal assemblages at Atna (top) and Li (bottom). Site scores are scaled as described in Table 1. The markers lying on top of each other are as follows: top left panel: 1996 and 1998; lower right panel: *Schizothrix* and *Phormidium* as well as *Chamaesiphon*, *Lemanea*, *Homoeothrix* and *Hydrurus foetidus*; stress values are 0.17 for Atna, and 0.18 for Li. Species are abbreviated as follows: Binu_tec = *Binuclearia tectorum*; Cham_con = *Chamaesiphon conferviculus*; Cham_ros = *Chamaesiphon rostafinskii*; Clas_set = *Clastidium setigerum*; Cyan_mir = *Cyanophanon mirabile*; Drap_glo = *Draparnaldia glomerata*; Hydr_foe = *Hydrurus foetidus*; Micr_amo = *Microspora amoena*; Micr_pal = *Microspora palustris*; Micr_pal_min = *Microspora palustris* var. *minor*; Moug_broad = *Mougeotia* > 12 mm; Moug_narrow = *Mougeotia* < 12 mm; Oedo_broad = *Oedogonium* > 20 mm; Oedo_narrow = *Oedogonium* < 20 mm; Scyt_sta = *Scytonematopsis starmachii*; all others are genus names.

	Atna				Li			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
PCA results								
Eigenvalue	12.334	9.277	5.896	5.367	17.569	8.981	7.069	5.905
Proportion Explained	0.213	0.160	0.102	0.093	0.275	0.140	0.111	0.092
Cumulative Proportion	0.213	0.373	0.474	0.567	0.275	0.415	0.525	0.618
PC scores for explanatory variables (scores > 0.5 or < -0.5 are marked in bold)								
Hydrology								
<i>mean discharge values</i>								
monthly mean discharge October [m3/sec]	-0.155	0.304	-0.045	0.080	0.208	-0.374	0.017	0.087
monthly mean discharge November [m3/sec]	-0.243	0.087	0.030	0.023	0.099	-0.029	0.189	-0.090
monthly mean discharge December [m3/sec]	-0.310	0.026	0.166	-0.164	0.064	0.104	0.112	-0.205
monthly mean discharge January [m3/sec]	-0.663	0.011	0.218	0.199	-0.343	-0.425	-0.197	-0.117
monthly mean discharge February [m3/sec]	-0.664	-0.058	0.262	0.048	-0.384	-0.390	-0.219	-0.121
monthly mean discharge March [m3/sec]	-0.540	-0.080	0.135	0.251	-0.416	-0.424	-0.179	-0.135
monthly mean discharge April [m3/sec]	-0.399	-0.016	0.064	-0.349	0.071	0.188	-0.061	-0.548
monthly mean discharge May [m3/sec]	-0.085	0.048	0.593	0.031	0.171	0.108	-0.301	0.343
monthly mean discharge June [m3/sec]	0.271	0.193	0.226	0.383	0.409	-0.186	0.221	-0.011
monthly mean discharge July [m3/sec]	-0.420	0.371	-0.125	0.219	0.175	-0.341	0.350	0.048
monthly mean discharge August [m3/sec]	-0.367	0.333	-0.067	-0.060	0.393	-0.164	0.277	0.051
monthly mean discharge September [m3/sec]	-0.172	0.475	-0.171	-0.338	0.414	-0.126	-0.018	-0.333
mean discharge October-September [m3/sec]	-0.476	0.430	0.307	0.124	0.466	-0.322	0.217	-0.091
median discharge October-September [m3/sec]	-0.661	0.127	0.130	-0.080	0.006	-0.066	0.134	-0.440
0.25 percentile discharge October-September [m3/sec]	-0.683	-0.045	0.208	0.168	-0.371	-0.413	-0.186	-0.155
0.75 percentile discharge October-September [m3/sec]	-0.557	0.464	0.018	0.014	0.390	-0.365	0.298	-0.137
<i>magnitude of annual extremes</i>								
one day maximum spring discharge [m3/sec]	0.385	0.198	0.520	0.175	0.637	-0.031	-0.047	-0.087
one day maximum discharge October-September [m3/sec]	0.420	0.231	0.479	0.098	0.637	0.084	-0.035	-0.041
one day minimum discharge October-September [m3/sec]	-0.650	-0.143	0.190	0.121	-0.433	-0.377	-0.223	-0.129
seven day maximum discharge October-September [m3/sec]	0.345	0.179	0.535	0.205	0.581	0.056	0.029	0.111
seven day minimum discharge October-September [m3/sec]	-0.652	-0.134	0.178	0.124	-0.427	-0.386	-0.224	-0.133
<i>timing of annual extremes</i>								
Julian day spring maximum (number)	0.017	0.286	-0.410	0.293	0.007	-0.152	0.481	0.065
Julian day October-September maximum (number)	0.005	0.238	-0.357	0.029	0.064	0.021	0.404	0.110
days between sampling and spring maximum (number)	0.221	-0.487	0.278	-0.281	-0.138	0.279	-0.434	-0.107
<i>frequency and duration of high pulses (high pulse defined as > 0.75 percentile discharge)</i>								
number of high pulses October-September (number)	-0.121	-0.055	-0.247	-0.194	0.009	0.148	-0.013	-0.410
average duration of high pulses October-September (number of days)	-0.267	0.378	0.228	0.226	0.235	-0.383	0.150	0.227
days of high pulse October-September (number of days)	-0.470	0.534	-0.043	0.069	0.485	-0.247	0.308	-0.111
<i>rate of change in flow</i>								
average rising limb October-September (number)	0.302	0.328	0.390	0.073	0.587	0.132	-0.027	0.075
maximum rising limb October-September (number)	0.424	0.277	0.222	-0.078	0.575	0.085	0.016	-0.126
average falling limb October-September (number)	-0.302	-0.396	-0.178	0.025	-0.514	-0.072	-0.103	-0.093
minimum falling limb October-September (number)	-0.469	-0.281	-0.425	-0.095	-0.592	-0.092	0.083	0.018
<i>base flow index (BFI)</i>								
	-0.596	-0.081	-0.175	-0.082	-0.556	-0.239	-0.058	0.019
Local climate								
<i>temperature</i>								
mean temp. October [°C]	-0.291	-0.134	-0.055	0.068	-0.179	0.050	0.457	0.076
mean temp. November [°C]	-0.324	-0.166	0.202	0.370	-0.293	-0.179	0.060	0.312
mean temp. December [°C]	-0.261	-0.478	-0.030	0.368	-0.493	-0.054	0.310	0.127
mean temp. January [°C]	-0.196	-0.398	0.053	-0.071	-0.264	0.274	0.304	-0.057
mean temp. February [°C]	-0.015	-0.501	0.313	-0.100	-0.443	0.325	-0.204	-0.020
mean temp. March [°C]	-0.205	-0.295	-0.233	0.088	-0.220	-0.002	0.037	-0.188
mean temp. April [°C]	-0.242	0.043	-0.164	-0.427	0.136	0.387	0.137	-0.353
mean temp. May [°C]	-0.353	-0.063	0.366	-0.267	-0.119	0.274	-0.296	0.047
mean temp. June [°C]	-0.077	-0.053	0.147	-0.258	0.102	0.267	0.253	-0.036
mean temp. July [°C]	0.126	0.089	-0.019	-0.215	0.279	0.191	0.236	0.255
mean temp. August [°C]	0.182	-0.115	-0.016	-0.272	-0.021	0.318	0.139	0.121
mean temp. September [°C]	-0.057	0.000	0.315	-0.404	0.019	0.241	-0.098	-0.028
mean temp. October-September [°C]	-0.394	-0.513	0.163	-0.125	-0.433	0.362	0.312	0.025
mean summer temp. (May-September) [°C]	-0.062	-0.004	0.265	-0.545	0.138	0.434	0.091	0.036
heat sum (> 0°C) May-September [degree-days]	-0.033	0.008	0.271	-0.538	0.139	0.417	0.065	0.044
minimum winter temperature [°C]	0.260	-0.503	0.192	-0.198	-0.296	0.468	-0.339	-0.066
<i>precipitation</i>								
precipitation October-September [mm]	-0.228	0.580	0.129	-0.250	0.337	-0.293	-0.006	-0.118
summer precipitation (May-September) [mm]	0.036	0.592	-0.006	-0.337	0.463	-0.162	-0.209	-0.300
number of days with precipitation>1mm during summer (May-September) (number of days)	-0.166	0.451	-0.018	-0.309	0.345	-0.057	-0.273	-0.450
maximum snow depth [cm]	-0.178	0.203	0.201	0.055	-0.050	0.020	-0.210	0.200
North Atlantic Oscillation (NAO)								
NAO (December-March) (number)	-0.153	-0.543	0.106	0.078	-0.384	0.266	0.097	-0.101
NAO (December-February) (number)	-0.157	-0.542	0.241	0.147	-0.334	0.280	0.091	0.051
NAO (March-May) (number)	-0.246	-0.170	-0.203	-0.371	-0.116	0.252	0.046	-0.460
NAO (July-August) (number)	0.435	-0.172	0.125	0.022	0.053	0.170	-0.143	0.507
NAO (September-November) (number)	-0.242	0.181	0.100	-0.150	0.307	0.170	0.060	-0.205
NAO (annual) (number)	-0.099	-0.285	0.132	-0.346	-0.044	0.508	0.010	-0.231
Suspended particles (only at "Li")								
<i>mineral particles</i>								
log maximum [mg/l]					0.545	0.174	-0.230	-0.024
log 95-percentile [mg/l]					0.460	0.089	-0.340	0.254
log average [mg/l]					0.538	0.111	-0.277	0.218
<i>organic particles</i>								
log maximum [mg/l]					0.529	-0.112	-0.243	-0.189
log 95-percentile [mg/l]					0.339	-0.070	-0.411	0.261
log average [mg/l]					0.316	-0.140	-0.422	0.132
Pearson correlations among response variables and PC axes (significant correlations marked in bold)								
NMDS1 (Atna: standardized to day 250)	-0.086	0.202	0.127	-0.020	-0.409	0.146	-0.060	0.114
NMDS2 (Li: standardized to day 250)	-0.114	-0.147	0.063	-0.012	0.587	-0.381	-0.175	-0.209
number of benthic algal taxa (Atna: standardized to day 250)	0.030	-0.122	-0.086	-0.245	-0.256	0.030	0.158	-0.209
log (total cover of benthic algae)	-0.468	-0.227	0.010	-0.268	-0.636	0.353	0.346	0.057
log (cover filamentous green algae)	-0.492	-0.142	-0.001	-0.253	-0.272	0.036	0.206	-0.105
log (cover Phormidium)	0.073	-0.160	-0.113	-0.179	-0.478	0.393	0.305	0.059
PIT-index (Li: standardized to day 250)	-0.126	-0.420	0.126	-0.344	0.068	-0.092	0.414	-0.091
Bray-Curtis dissimilarity among consecutive years	-0.146	-0.043	-0.339	-0.127	0.392	-0.260	-0.260	-0.058

Table S1 PCA results for environmental parameters, scores for explanatory variables along PC axes, and Pearson correlation coefficients among response parameters and the PC axes; significant values are marked in red.

1

NMDS1 model NMDS1_stand250 = -1.493 + 0.852*7day_min_q.year-1 explanatory variable 7-day min q.year-1 Interpretation	Adjusted R-squared: 0.245 other variables corr. with this expl. variable and with NMDS1 mean_q_mar-year-1, 25perc_q_year-1, min_q_year-1 Interpretation	F-statistic: 7.49 on 1 and 19 Df, p-value: 0.01311 sum of squares 1.757 Pr(>F) 0.0131	length of time series (years) 21 Pr(>F) 0.0131
NMDS2 model NMDS2 = -3.60 + 4.93*BFI.year-1 explanatory variable BFI year-1 Interpretation	Adjusted R-squared: 0.273 other variables corr. with this expl. variable and with NMDS2 none Interpretation	F-statistic: 8.491 on 1 and 19 Df, p-value: 0.008903 sum of squares 1.249 Pr(>F) 0.0089	length of time series (years) 21 Pr(>F) 0.0089
number of taxa model n_taxa_stand250 = 32.76 - 1.564*mean_temp_june explanatory variable mean_temp_june Interpretation	Adjusted R-squared: 0.2067 other variables corr. with this expl. variable and with n_taxa none Interpretation	F-statistic: 6.211 on 1 and 19 Df, p-value: 0.0221 sum of squares 78.302 Pr(>F) 0.0221	length of time series (years) 21 Pr(>F) 0.0221
total cover of benthic algae model log_tot_cov = 0.639 + 0.100*mean_temp_apr + 0.477*min_q explanatory variable mean_temp_apr min_q Interpretation	Adjusted R-squared: 0.440 other variables corr. with this expl. variable and with total cover mean_fa_limb mean_q_feb, 7day_min_q, mean_ann_temp, spring_max_q_year-1, min_fa_limb-year-1 Interpretation	F-statistic: 8.84 on 2 and 18 Df, p-value: 0.002116 sum of squares 0.836 0.544 Pr(>F) 0.0043 0.0166	length of time series (years) 21 Pr(>F) 0.0043 0.0166
cover of filamentous green algae model log_filgreen = 0.785 - 0.19396*NAO_JJA + 0.036*mean_q_aug.year-1 explanatory variable NAO_JJA mean_q_aug-year-1 Interpretation	Adjusted R-squared: 0.463 other variables corr. with this expl. variable and with total cover of fil. green algae none Interpretation	F-statistic: 9.623 on 2 and 18 Df, p-value: 0.001438 sum of squares 1.222 0.679 Pr(>F) 0.0015 0.0173	length of time series (years) 21 Pr(>F) 0.0015 0.0173
cover of Phormidium model log_Phorm = -0.381 + 0.0027*date_max_q_year-1 explanatory variable date_max_q_year-1 Interpretation	Adjusted R-squared: 0.183 other variables corr. with this expl. variable and with cover of Phormidium none Interpretation	F-statistic: 5.486 on 1 and 19 Df, p-value: 0.03022 sum of squares 0.992 Pr(>F) 0.0302	length of time series (years) 21 Pr(>F) 0.0302
periphyton index of trophic status (PIT) model PIT = 4.655 + 0.313*mean_ann_temp + 0.0195*max_ris_limb.year-1 explanatory variable mean_ann_temp max_ris_limb-year-1 Interpretation	Adjusted R-squared: 0.530 other variables corr. with this expl. variable and with PIT mean_temp_aug, mean_sum_temp, heat_sum none Interpretation	F-statistic: 12.27 on 2 and 18 Df, p-value: 0.0004354 sum of squares 1.452 0.925 Pr(>F) 0.0011 0.0063	length of time series (years) 21 Pr(>F) 0.0011 0.0063
Bray-Curtis dissimilarity between consecutive years Bray dissimilarity between consecutive years was not related to any of the measured variables			

2

3 **Table S2a** results of multivariate linear models for the site Atna; q = discharge, BFI = base
 4 flow index, NAO_JJA = North Atlantic Oscillation_June-July-August, year-1 = additional
 5 time lag of one year; all other abbreviations should be self-explanatory after consulting Table
 6 2.

NMDS1 model NMDS1 = 0.5357 + 0.1183*mean_temp_apr.year-1 - 0.0062*max_snow_depth.year-1 explanatory variable mean_temp_apr.year-1 max_snow_depth.year-1 Interpretation	Adjusted R-squared: 0.426 other variables corr. with this expl. variable and with NMDS1 NAO_max_snow_depth_year-1 mean_temp_apr_year-1 Interpretation	F-statistic: 9.916 on 2 and 22 Df, p-value: 0.00085 sum of squares 1.4254 0.5817 Pr(>F) 0.0011 0.0254	length of time series (years) 25 Pr(>F) 0.0011 0.0254
NMDS2 model NMDS2_stand250 = -0.4544 + 0.612*log_max_org_part - 0.110*NAO_DIF_year-1 explanatory variable log_max_org_part NAO_DIF_year-1 Interpretation	Adjusted R-squared: 0.573 other variables corr. with this expl. variable and with NMDS2 spring_max_q, max_ris_limb, mean_temp_dec, mean_ann_temp, sum_sum_prec, n_rain_days, NAO_DIF, log_max_min_part, log_95perc_min_part, log_mean_org_part, log_max_min_part, n_rain_days, mean_temp_jan-year-1, mean_temp_feb-year-1, sum_sum_prec-year-1, NAO_DIFM-year-1, NAO-year-1, log_max_org_part-year-1 Interpretation	F-statistic: 15.1 on 2 and 19 Df, p-value: 0.000119 sum of squares 0.9277 0.3947 Pr(>F) 0.0002 0.0073	length of time series (years) 22 Pr(>F) 0.0002 0.0073
number of taxa model n_taxa = 21.265 + 0.877*mean_temp_dec_year-1 explanatory variable mean_temp_dec_year-1 Interpretation	Adjusted R-squared: 0.291 other variables corr. with this expl. variable and with n_taxa none Interpretation	F-statistic: 10.86 on 1 and 23 Df, p-value: 0.00316 sum of squares 98.715 Pr(>F) 0.0032	length of time series (years) 25 Pr(>F) 0.0032
total cover of benthic algae model log_tot_cov = 2.1884 - 1.1899*log_mean_org_part - 1.395*log_95perc_org_part_year-1 explanatory variable log_mean_org_part log_95perc_org_part_year-1 max_snow_depth_year-1 Interpretation	Adjusted R-squared: 0.737 other variables corr. with this expl. variable and with total cover spring_max_q, max_q, max_ris_limb, mean_temp_dec, sum_sum_prec, log_max_min_part, log_95perc_min_part, log_mean_min_part, log_max_org_part, log_95perc_org_part max_q, max_ris_limb, mean_ann_temp, sum_sum_prec, n_rain_days max_ris_limb, mean_ann_temp_year-1 high concentrations of (organic) particles (associated with floods) and more snow (= lower annual temperatures) lead to decreased algal cover; flood effects occurred in the same year, while snow (temperature) effects occurred after a time lag of one year Interpretation	F-statistic: 20.58 on 3 and 18 Df, p-value: 4.787e-06 sum of squares 0.8823 0.6965 0.4488 Pr(>F) 6.3E-05 2.2E-04 1.7E-03	length of time series (years) 22 Pr(>F) 0.0002 0.0266
cover of filamentous green algae model log_filgreen = 1.321 - 1.506*log_95perc_org_part_year-1 - 0.705*log_mean_org_part explanatory variable log_95perc_org_part_year-1 log_mean_org_part Interpretation	Adjusted R-squared: 0.460 other variables corr. with this expl. variable and with total cover of fil. green algae sum_sum_prec, n_rain_days log_max_min_part, log_95perc_min_part, log_mean_min_part, log_max_org_part high concentrations of (organic) particles (associated with floods) decreased the cover of filamentous green algae Interpretation	F-statistic: 9.959 on 2 and 19 Df, p-value: 0.0011 sum of squares 0.6439 0.2631 Pr(>F) 0.0013 0.0266	length of time series (years) 22 Pr(>F) 0.0013 0.0266
cover of Phormidium model log_Phorm = 3.239 - 0.306*75perc_q_year-1 - 0.018*max_snow_depth_year-1 explanatory variable max_snow_depth_year-1 75perc_q_year-1 Interpretation	Adjusted R-squared: 0.703 other variables corr. with this expl. variable and with cover of Phormidium mean_ann_temp_year-1 duration_high_pulse_year-1, days_high_pulse_year-1 prolonged periods of high discharge decreased Phormidium cover (substrate movement), while less snow (high annual temperatures) increased Phormidium cover; effects occur after a time lag of one year Interpretation	F-statistic: 16.37 on 2 and 11 Df, p-value: 0.000505 sum of squares 1.4895 1.3410 Pr(>F) 0.00162 0.00232	length of time series (years) 14 Pr(>F) 0.00162 0.00232
periphyton index of trophic status (PIT) model PIT_stand250 = 3.8645 + 0.00959*date_max_q_year-1 - 1.0093*mean_q_jan + 0.00256*sum_prec_year-1 explanatory variable date_max_q_year-1 mean_q_jan sum_prec_year-1 Interpretation	Adjusted R-squared: 0.667 other variables corr. with this expl. variable and with PIT 25perc_q n_rain_days, min_wint_temp_year-1, sum_sum_prec_year-1, NAO_DIF_year-1 late floods, low discharge (especially in January) and high precipitation lead to more eutrophic algal assemblages; effect partly occurred after a time lag of one year Interpretation	F-statistic: 10.33 on 3 and 11 Df, p-value: 0.00157 sum of squares 0.9632 0.7197 0.5418 Pr(>F) 3.687E-03 9.195E-03 1.879E-02	length of time series (years) 15 Pr(>F) 3.687E-03 9.195E-03 1.879E-02
Bray-Curtis dissimilarity between consecutive years model Bray = -0.3525 + 0.2249*mean_q + 0.591*log_mean_org_part explanatory variable mean_q log_mean_org_part Interpretation	Adjusted R-squared: 0.590 other variables corr. with this expl. variable and with Bray mean_q_aug, 75perc_q_duration_high_pulse, days_high_pulse, sum_sum_prec, log_max_org_part mean_temp_dec, log_max_min_part, log_95perc_min_part, log_mean_min_part, log_max_org_part, log_95perc_org_part high average and maximum discharge (particle concentrations) caused unstable benthic algal assemblages Interpretation	F-statistic: 10.36 on 2 and 11 Df, p-value: 0.00296 sum of squares 0.3444 0.1390 Pr(>F) 0.0027 0.0328	length of time series (years) 14 Pr(>F) 0.0027 0.0328

7

8 **Table S2b** results of multivariate linear models for the site Li; q = discharge, NAO_DJF =
 9 North Atlantic Oscillation_December-January-February, year-1 = additional time lag of one
 10 year; all other abbreviations should be self-explanatory after consulting Table 2.

