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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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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

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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 km^2. 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 μg/l, respectively (unpublished data). Calcium concentrations at the sampling sites are generally below 1 mg/l, and conductivity is usually well below 10 μS/cm (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

2.2.1. 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 740 m, 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 × 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