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1 **Effects of flow regime on benthic algae and macroinvertebrates - a comparison between**
2 **regulated and unregulated rivers**

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14 **Running title**

15 Effects of river flow on benthic algae and macroinvertebrates

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20 **Keywords**

21 stream; benthic algae; periphyton; macroinvertebrates; discharge; heavily modified water
22 bodies

23 **Abstract**

24 Natural fluctuations in flow are important for maintaining the ecological integrity of riverine
25 ecosystems. However, the flow regime of many rivers has been modified. We assessed the
26 impact of water chemistry, habitat and streamflow characteristics on macroinvertebrates and
27 benthic algae, comparing 20 regulated with 20 unregulated sites. Flow regime, calculated
28 from daily averaged discharge over the five years preceding sampling, was generally more
29 stable at regulated sites, with higher relative discharges in winter, lower relative discharges in
30 spring and smaller differences between upper and lower percentiles. However, no consistent
31 differences in benthic algal or macroinvertebrate structural and functional traits occurred
32 between regulated and unregulated sites. When regulated and unregulated sites were pooled,
33 overall flow regime, calculated as principal components of discharge characteristics over the
34 five years preceding sampling, affected macroinvertebrate species assemblages, but not
35 indices used for ecosystem status assessment or functional feeding groups. This indicates that,
36 while species identity shifted with changing flow regime, the exchanged taxa had similar
37 feeding habits. In contrast to macroinvertebrates, overall flow regime did not affect benthic
38 algae. Our results indicate that overall flow regime affected the species pool of
39 macroinvertebrates from which recolonization after extreme events may occur, but not of
40 benthic algae. When individual components of flow regime were analyzed separately, high
41 June (i.e. three months before sampling) flow maxima were associated with low benthic algal
42 taxon richness, presumably due to scouring. Macroinvertebrate taxon richness decreased with
43 lower relative minimum discharges, presumably due to temporary drying of parts of the
44 riverbed. However, recolonization after such extreme events presumably is fast. Generally,
45 macroinvertebrate and benthic algal assemblages were more closely related to water physico-
46 chemical than to hydrological variables. Our results suggest that macroinvertebrate and
47 benthic algal indices commonly used for ecological status assessment are applicable also in
48 regulated rivers.

49

50 **1. Introduction**

51 Environmental gradients shape river ecosystems along with disturbances such as floods and
52 droughts, and the flow regime is often regarded to be a key driver of river ecosystems (Poff et
53 al., 1997; Bunn and Arthington, 2002). Substantial variability exists in natural river flow
54 characteristics, which are related to climate, geology and topography, and natural fluctuations
55 in river flow are fundamentally important for the long-term sustainability and productivity of
56 riverine ecosystems, i.e. for the maintenance of their ecological integrity (Poff et al. 1997;
57 Naiman et al., 2008). However, the flow regime of many rivers has been modified, e.g. by
58 dampening or eliminating natural floods and droughts in order to meet human needs such as
59 transport, water supply, flood control or hydropower (Dynesius and Nilsson, 1994; Gleick,
60 2003). This may negatively affect river ecosystems, and indeed hydraulic engineering is, next
61 to pollution from agriculture, regarded as the main factor inhibiting the achievement of good
62 ecological status of European river basins (Menendez et al., 2006).

63 Hydropower is an important global source of electricity (Gracey and Verones, 2016). In
64 Norway, almost all electricity is generated from hydropower plants (Linnerud and Holden,
65 2015), causing about 70% of river catchments to be affected by regulation (www.nve.no).
66 Apart from mandatory minimum flow releases, release of water from hydropower reservoirs
67 depends on short- and long-term electricity demand, such that river flow may undergo
68 fluctuations that differ from the natural flow regime (Kern et al., 2012).

69 The flow regime of rivers and streams can be identified by several streamflow characteristics
70 which are deemed ecologically important; seasonal flow pattern, timing and magnitude of
71 extreme flows, frequency and duration of flow extremes and rate of change (Olden and Poff,
72 2003). Alterations to these streamflow characteristics may affect the structure and function of
73 rivers and contribute to the loss of biodiversity (Bunn and Arthington 2002). The
74 consequences of natural variation and anthropogenic modifications in flow to riverine
75 ecosystems have been relatively well studied (Rolls et al., 2012). For example, streamflow
76 variability affects fish assemblages and traits (Poff and Allan, 1995; Murchie et al. 2008).
77 Likewise, macroinvertebrate assemblages and traits are affected by droughts (Monk et al.,
78 2008; Bonada et al. 2007), but also by summer flow characteristics and by short-term
79 hydrological events (Extence et al., 1999). Mass developments of submerged macrophytes in
80 regulated rivers have been related to enhanced winter discharges (which cause less freezing
81 damage; Johansen et al., 2000). However, conflicting results have also been reported. For
82 benthic algal assemblages, increases as well as decreases in biomass after large floods have

83 been observed (Power et al., 2008; Schneider, 2015), macrophyte mass developments occur in
84 some but not other rivers having enhanced winter discharges (Johansen et al., 2000), and wide
85 variation is displayed in the severity and direction of responses of fishes to river regulation
86 (Murchie et al., 2008). The varying response of biota after extreme events may partly be
87 explained by recolonization. For example, even if short term spates can decrease the
88 abundance and diversity of macroinvertebrates (Scrimgeour et al., 1988), recovery is often
89 rapid, presumably due to colonization from flow refuges, or from aerial ovipositing adults
90 (Müller, 1982; Palmer et al. 1992). Also adaptations, for example in life history, behavior, or
91 morphology (Lytle, 2002; Lytle and Poff, 2004), may contribute to explaining varying
92 responses of the biota after extreme events. In addition, covariation of flow regime with other,
93 potentially influential parameters such as water chemistry may lead to unexplained variation
94 in the biological response.

95 However, even though we like to think that the consequences of natural variation and
96 anthropogenic modifications in flow are relatively well understood, present knowledge on the
97 effects of river flow on aquatic biota is to a large degree based on studies covering a relatively
98 short time-scale (Monk et al., 2008). Such studies predict site-specific short-term effects of
99 river flow, but do not allow inferences to which degree the species pool from which
100 recolonization may occur is affected. However, this is important in order to distinguish
101 between short-term effects of disturbances which soon may be ameliorated because
102 recolonization is fast, and long-lasting consequences for the ecosystem. Comparative studies
103 on the long-term effects of flow regime on aquatic biota are, however, usually based on
104 spatially diverse datasets. This may lead to covariation between flow regime and other
105 potentially influential parameters, e.g. climate and hydrochemistry. Such potentially
106 confounding factors have often been ignored, presumably due to a lack of data (Clausen and
107 Biggs, 1997; Petrin et al., 2013). Studies that included river flow as well as water chemistry
108 concluded that both direct changes in river flow or indirect changes in water quality may be
109 important for river biota (Sheldon and Thoms, 2006; Greenwood et al., 2016). River
110 regulation does not only modify flow regime, but may also affect water quality due to factors
111 such as the transfer of water between river catchments, or the discharge of hypolimnic
112 reservoir water into rivers (Gracey and Verones, 2016). Consequently, river regulation may
113 affect biota via changes in flow regime, or via changes in water quality. For planning effective
114 remediation measures, it is important to distinguish effects of flow regime from effects of
115 water quality on river biota.

116 Deterioration and improvement of river ecological status in Europe is determined by
117 comparing the biota that occur at a site with those that occur at unimpacted reference sites
118 (EC, 2000). However, river biota respond to many parameters, including hydrochemistry and
119 different aspects of flow regime. This is particularly relevant in so-called Heavily Modified
120 Water Bodies (HMWB). River reaches can be designated as HMWB if applying the
121 hydromorphological measures to reach good ecological status would significantly affect water
122 uses (e.g. flood protection, hydropower generation). The environmental objectives for
123 HMWB can be lowered to good ecological potential (GEP) which corresponds to the state
124 that results from applying all hydromorphological measures that may improve ecological
125 status but at the same time do not significantly affect water uses (Kail and Wolter, 2013). This
126 means that, if river regulation for hydropower generation should consistently affect river
127 biota, the environmental objectives for such rivers could be lowered. We therefore wanted to
128 know (i) whether there occur systematic differences in assemblages of macroinvertebrates and
129 benthic algae, i.e. organisms commonly used for ecological status evaluation, between
130 regulated and unregulated rivers, and (ii) how flow regime affects macroinvertebrates and
131 benthic algae.

132 We assessed the impact of streamflow characteristics (calculated from five years of daily
133 averaged discharge data), water chemistry and habitat characteristics on macroinvertebrate
134 and benthic algal structural and functional traits, comparing 20 regulated sites (= modified
135 flow regime) with 20 unregulated sites (= natural flow regime). It has been shown before that
136 disturbance regime affects taxon richness (Townsend et al., 1997) and changes competitive
137 interactions among species and age classes (Feminella and Resh, 1990). We therefore
138 hypothesized that (1) regulated sites would have a more stable flow regime than unregulated
139 sites, leading to fewer macroinvertebrate and benthic algal taxa in regulated than in
140 unregulated sites, and (2) flow regime would shape macroinvertebrate and benthic algal
141 assemblages, with communities adapted to low flow conditions occurring at sites with a stable
142 flow regime.

143

144 **2. Material and Methods**

145 **2.1 Sampling sites**

146 The Norwegian Water Resources and Energy Directorate (NVE) operates a network of
147 hydrological gauging stations (Petterson, 2004). From these sites, we selected 20 which were

148 situated in regulated rivers in South Norway (Fig. 1). Criteria for site selection were i)
149 availability of daily averaged discharge data since 2008, ii) independence of sites, i.e. no site
150 was located downstream from another regulated site, and iii) accessibility for sampling. All
151 20 sites have been regulated for ≥ 25 years (Table A.1 in the appendix), i.e. we expected
152 riverine biota to have adjusted to the modified flow regime. We then selected 20 unregulated
153 sites, based on the same criteria as the regulated sites, and attempted to match the geographic
154 spread of the regulated sites as closely as possible (because climate varies in South Norway,
155 with generally wetter and warmer conditions in the South-West (Moreno and Hasenauer,
156 2016). However, some compromises had to be made, such that two of the unregulated sites
157 lay in the same river (but with a large lake in between, such that these two sites had quite
158 different flow regimes). River regulation is a multifaceted term, and also the 20 regulated sites
159 in our dataset were subject to different main effects of regulation. Our dataset includes so-
160 called “minimum discharge” sites, i.e. sites from which stream water is abstracted and
161 bypasses the river, so that the amount of water remaining in the stream is reduced; in addition,
162 our dataset includes sites situated downstream the outlet of hydropower plants and sites that
163 were situated downstream dams. In an earlier version of our manuscript, “minimum
164 discharge” and “downstream outlet hydropower plant” sites were analyzed separately.
165 However, since this did not provide additional important information, the regulated sites were
166 pooled.

167 All 40 sites were visited once between September 2 and September 16, 2013, and samples of
168 stream water, benthic algae and benthic macroinvertebrates were taken. In September, which
169 in Scandinavia is early autumn, benthic algal biomass does not yet show signs of senescence,
170 while macroinvertebrate larvae have developed far enough to be countable. Early autumn
171 samples are commonly used for ecological status assessment in Northern European rivers.
172 Samples were taken as close as possible to the respective hydrological gauging stations; this
173 was in all cases less than 1 km from the gauging station. No tributaries were present between
174 the gauging stations and the respective sites where the samples were collected.

175

176 **2.2 Data collection**

177 *Benthic algae*

178 At each site, benthic algae were collected from two replicate sub-sites located in riffles,
179 situated approximately 25 m apart. Chlorophyll *a* (in $\mu\text{g Chl-}a/\text{cm}^2$) at each sub-site was

180 measured from the upper side of five cobbles (with a diameter of approximately 10 cm) using
181 a BenthosTorch, i.e. a Pulse Amplitude Modulated (PAM) fluorimeter developed by BBE
182 Moldaenke GmbH. In Swedish streams, the BenthosTorch has been shown to give similar
183 readings for epilithic Chl *a* as conventional methods (Kahlert and McKie, 2014). Samples of
184 soft-bodied benthic algae (= algae including cyanobacteria attached to the river bottom or in
185 close contact on or within patches of attached aquatic plants, but excluding diatoms) were
186 taken according to European standard procedures (EN 15708:2009) along an approximately
187 10-m length of river bottom using an aquascope (i.e. a bucket with a transparent bottom). At
188 each sub-site, cover (%) of each form of macroscopically visible benthic algae was recorded,
189 and samples were collected and stored separately in vials for species determination. In
190 addition, microscopic algae were collected from ten cobbles/stones with diameters ranging
191 between approximately 10 and 20 cm, taken from each site. An area of about 8 x 8 cm from
192 the upper side of each cobble/stone was brushed with a toothbrush to transfer the algae into a
193 beaker containing approximately 1 L of river water from which a subsample was taken. All
194 samples were preserved with a few drops of formaldehyde to a final concentration of
195 approximately 0.5%. The preserved benthic algae samples were later examined under a
196 microscope (200 - 600 × magnification) and all non-diatom algae identified to species,
197 wherever possible. For some genera of filamentous green algae whose vegetative forms
198 cannot be determined to species level (e.g. *Spirogyra* Link or *Mougeotia* C. Agardh)
199 categories based mainly on filament width were used (see Schneider and Lindstrøm (2009;
200 2011) for further details). The primary identification keys used were Komarek and
201 Anagnostidis (2007), Gutowski and Förster (2009), John et al. (2011) and Komarek (2013).
202 Abundance of each microscopic taxon was estimated in the laboratory as “rare”, “common”
203 and “abundant”. These estimates were later translated into % cover as 0.001, 0.01 and 0.1%,
204 respectively. Macroscopic algae whose cover was recorded as “<1%” in the field, were noted
205 as “0.1%” for data analysis. For all other taxa, the cover that was estimated in the field was
206 used. Total algal cover was calculated as the sum of cover of all taxa. Note that % algal cover
207 includes all types of substrate (including for example algae that grew epiphytic on
208 bryophytes) but does not include diatoms, while Chl *a* measured with BenthosTorch captured
209 exclusively epilithic algae, but included diatoms.

210

211 ***Macroinvertebrates***

212 At each site, an approximately 50 m long reach was delimited, where we collected ten
213 replicate benthic samples using a Surber net (sampling area: 0.1 m², mesh size: 500 µm). For
214 sampling, the substrate was agitated to a depth of ca. 10 cm for one minute. All benthic
215 samples were immediately preserved in 70 % ethanol and later analyzed in the laboratory. At
216 most sampling locations, the substrate mainly comprised gravel, pebbles, cobbles or small
217 boulders, although at some sites wood, twigs, cones, conifer needles, leaf fragments, aquatic
218 mosses and macrophytes were also recorded. Some of the bed material was partly embedded
219 in several reaches, and boulders interspersed the substrate in other reaches. In the laboratory,
220 all benthic samples were sorted using a 500 µm sieve. The benthic macroinvertebrates were
221 classified to the lowest possible taxonomic level, usually species. However, some dipteran
222 taxa and microcaddisflies (Hydroptilidae) could only be identified to genus. In addition,
223 bryozoans, nematodes, oligochaetes, water mites, cladocerans, ostracods, non-biting midges
224 and blackflies could not be identified further.

225

226 *Environmental variables*

227 Hydrological data (discharge in m³ s⁻¹) have been recorded by the Norwegian Water
228 Resources and Energy Directorate (NVE), and are stored in the HYDRA II database. For each
229 site, available discharge data from the five years preceding sampling, i.e. from September 1,
230 2008 to August 31, 2013, were extracted from the database as daily averaged values. For one
231 site (site number 25.6, Table S1), data from 2009 were lost, meaning that hydrological
232 characteristics for this site were calculated based on four years of data only. Malfunctioning
233 of the dataloggers caused 13 short gaps in the hydrological data (with an average duration of 9
234 days). Since we had no indication that any extraordinary flow events occurred during these
235 short gaps, the discharge for these days was estimated by linear interpolation between the last
236 day before the onset of malfunctioning and the first day after the malfunctioning datalogger
237 was replaced/fixed. One gap of 172 days was estimated by interpolation from another gauging
238 station close by. Apart from that, the hydrological data for all 40 sites were complete for the
239 period of 5 years.

240 In addition to hydrological regime, we collected data on (i) geographic location and
241 catchment characteristics (latitude, longitude, altitude, catchment size, distance to nearest
242 lake/reservoir upstream; these data were either taken from Petterson (2004) or recorded from
243 a digital map of Norway); (ii) water physico-chemistry (Calcium (Ca): NS EN ISO 11885;

244 total organic carbon (TOC): NS EN 1484; Total phosphorus (TotP): NS EN ISO 15681-2;
245 Total nitrogen (TotN): NS 4743); in addition, temperature, pH and conductivity were
246 measured with hand-held instruments); and (iii) site characteristics ((a) average water depth
247 where the samples were taken; (b) stream width; (c) shading (estimate between 0 = no
248 shading and 1 = full shade under trees); (d) % turbulent flow; (e) % cover of boulders (>20
249 cm), cobbles (6-20 cm), gravel (2-6 cm), fine gravel (2mm – 6 cm), and sand (0.1 – 2 mm);
250 (f) % cover of coarse (> 1 mm) and fine (< 1mm) particulate organic matter (CPOM and
251 FPOM) covering the sediment; (g) % cover of bryophytes and macrophytes).

252

253 **2.3 Data treatment and statistics**

254 *Benthic algae and macroinvertebrates*

255 To explore species composition and abundance of the macroinvertebrate and benthic algal
256 assemblages, respectively, an NMDS (non-metric multidimensional scaling) was computed
257 on square-root transformed data. NMDS was used because, in contrast to other ordination
258 methods, it can also handle non-linear responses. The NMDS was computed using the meta
259 MDS function in R, version 2.14.2 (R Development Core Team, 2012), extended with the
260 “vegan” package 2.0-4 (Oksanen et al., 2012). Bray–Curtis was used as the dissimilarity
261 measure because it is less dominated by single large differences than many other dissimilarity
262 measures (Quinn and Keough, 2002). In addition to NMDS scores, the following response
263 parameters were calculated from the macroinvertebrate and benthic algal taxon lists: (1) taxon
264 richness of macroinvertebrates and benthic algae, respectively; (2) total cover of benthic algae
265 (calculated as sum of cover of all taxa) and density of macroinvertebrates (individuals/m²);
266 (3) cover of cyanobacteria having heterocysts (because they reflect the potential for N-
267 fixation (Stancheva et al., 2013); (4) the number of macroinvertebrate individuals in the
268 functional feeding groups shredders (feeding on coarse particulate organic matter (CPOM)),
269 gatherer/collectors (feeding on fine particulate organic matter (FPOM)), grazers/scrapers
270 (feeding on periphyton), and filter feeders (feeding on suspended organic matter), following
271 ASTERICS 4.0.4 (2014), because they provide a link to ecosystem processes; (5) the AIP-
272 index (“Acidification Index Periphyton”; Schneider and Lindstrøm, 2009) and the
273 acidification index “Raddum 2” (Raddum and Fjellheim, 1984; Raddum 1999) because they
274 provide a link to the acidity tolerance of the benthic algal and macroinvertebrate assemblages,
275 respectively; (6) the PIT (Periphyton Index of Trophic Status; Schneider and Lindstrøm,

276 2011) and ASPT (Average Score Per Taxon; Armitage et al., 1983), because they provide a
277 link to eutrophication and ecological status assessment; (7) the LIFE index (Lotic-invertebrate
278 Index for Flow Evaluation; Extence et al., 1999) was calculated based on macroinvertebrate
279 assemblages using ASTERICS (2014), because it describes flow-preferences of benthic
280 invertebrate assemblages. Other response parameters were calculated (e.g. cover of red algae,
281 cover of *Phormidium* sp., diversity indices, relative occurrence of functional feeding groups,
282 taxonomic groups such as the number of Ephemeroptera/Plecoptera/Trichoptera, etc.), but
283 omitted from further analysis since they either only occurred in low abundances, or co-varied
284 with other response parameters. After exploratory analysis, data were log (x+1)-transformed
285 where necessary to improve normality and homoscedasticity (Table 1). For river biota, results
286 of the two benthic algal and ten macroinvertebrate samples per site were averaged, and linear
287 models were computed using the MASS-package in R (Venables and Ripley, 2002).
288 However, we also tested linear mixed models on the complete dataset (including two replicate
289 benthic algal samples per site, and 10 replicate macroinvertebrate samples per site), using the
290 nlme-package in R (Pinheiro et al., 2012), and “site” was included as random factor. In order
291 to enable unbiased comparisons of the response variables between regulated and unregulated
292 sites, their values had to be corrected for the differences in explanatory variables that occurred
293 between regulated and unregulated sites (i.e. catchment size, altitude, TN and TOC; the last
294 three also correlated with each other). In order to do so, we computed a set of multivariate
295 linear models, separately for each response variable that was significantly correlated with one
296 or several of the explanatory variables whose values significantly differed between regulated
297 and unregulated rivers. We then selected, separately for each response variable, the best
298 model by using an information-theoretic approach (Akaike information criterion; AIC), and
299 corrected the value of each response variable based on the slope of the respective best model.

300

301 ***Environmental variables***

302 At one site, we forgot to record conductivity and temperature (NVE number 36.32; Table
303 A.1). The missing values were estimated from the variables that correlated closest with
304 conductivity and temperature at the remaining 39 sites (i.e. a linear correlation between log
305 (conductivity) and log (Calcium) (Pearson $r = 0.94$; $R^2=0.88$), as well as temperature and log
306 (TOC) (Pearson $r = 0.78$; $R^2=0.62$)). In order to characterize sediment composition at each
307 site, a PCA (principal component analysis) was calculated from the scaled data on % cover of
308 boulders, cobbles, gravel, fine gravel, sand, CPOM, FPOM and bryophytes, using the vegan-

309 package in R. The first two axes explained 55% of variation; PC1 was positively related with
310 boulders and bryophytes, and negatively with cobbles and gravel; PC2 was positively related
311 with fine gravel, sand and cover of CPOM (Table A.2).

312 Richter et al. (1996) defined several “indicators of hydrologic alteration” to statistically
313 characterize variation in river flow. They are categorized into the following five groups,
314 which are considered useful to quantitatively evaluate the impact of hydrological regime on
315 aquatic biota: (1) mean discharge values, (2) magnitude of annual extremes, (3) timing of
316 annual extremes, (4) frequency and duration of high and low pulses, and (5) rate of change.
317 We calculated 77 variables from the daily averaged discharge values, which were assigned to
318 these five categories (Table 1). In addition, the base flow index (= the ratio of base flow to
319 total streamflow) was calculated using the “lf stat”-package in R (Koffler, 2013). In order to
320 enable comparisons among sites (i.e. independent of river size), the values for the “indicators
321 of hydrologic alteration” at each site were calculated relative to the average discharge during
322 the five years preceding sampling. In order to capture effects of both “long-term” flow
323 regime, as well as recent events, all streamflow characteristics were calculated for the total
324 period of five years preceding sampling of benthic algae and macroinvertebrates (“long-
325 term”), and in addition for the one year preceding sampling (“recent”).

326 Together with site characteristics and water chemistry, 97 environmental variables were
327 compiled for each site. After exploratory analysis, data were transformed where necessary to
328 improve normality and homoscedasticity (Table 1). Prior to data analysis, we inspected scatter
329 plots in order to search for possible non-linear (e.g. hump-shaped) relationships. No
330 indications of such patterns were found, however. We used ANOVA to compare regulated
331 with unregulated sites. In order to analyze the influence of overall flow regime on each
332 response variable, we summarized the 78 hydrological variables into principal components
333 using the vegan-package in R. However, because each principal component represents a
334 plethora of hydrological variables whose individual importance for the response parameters
335 cannot be deduced, we also calculated a correlation matrix between explanatory and response
336 variables. We then summarized the strongest correlations and interpreted their importance
337 against the background of published information.

338

339 **3. Results**

340 **3.1 Differences between regulated and unregulated sites**

341 We attempted to select our sampling sites in such a way that no environmental variable except
342 flow regime would differ between regulated and unregulated sites. However, this was not
343 possible, since the position of the hydrological gauging stations obviously was tailored to the
344 management needs of the Norwegian Water Resources and Energy Directorate, and not to our
345 project. As a consequence, the regulated sites in our dataset not only differed in flow regime
346 from unregulated sites, but they also had a larger watershed, were situated at a lower altitude,
347 and had slightly higher TN and TOC concentrations (Table 1). Apart from that, only river
348 flow differed between regulated and unregulated sites, with regulated sites having higher
349 relative discharges in winter, lower relative discharges in spring, and smaller differences
350 between upper and lower percentiles (see Table 1 for summary statistics, and Table A.6 for a
351 complete overview over hydrological characteristics at each sampling site). After accounting
352 for the differences in catchment size, altitude, TN and TOC (Table A.3), none of the response
353 variables differed between regulated and unregulated sites, despite the differences that
354 occurred in river flow (Table 1).

355 We then used PCA to summarize the 78 hydrological variables into principal components,
356 reflecting overall flow regime. The first two PCs explained 55% of the variation in
357 hydrological variables (Table A.5). High scores along PC1 corresponded to streams with
358 relatively high winter discharges, generally low 7-day maxima, and small differences between
359 upper and lower percentiles, i.e. high scores along PC1 characterized sites with a
360 comparatively “stable” flow regime. High scores along PC2 corresponded to a hydrological
361 regime dominated by run-off (a low BFI indicates a high contribution of run-off (and a low
362 contribution of base-flow) to total streamflow), steeply rising and falling limbs, and relatively
363 high autumn discharges (Table A.5), i.e. high scores along PC2 characterized “flushy” rivers.
364 Higher principal components explained little of the total variation (no axis explained more
365 than 10%), and few strong relationships with explanatory variables occurred (data not shown),
366 such that higher PC axes could not be meaningfully interpreted. Although there was
367 considerable overlap, regulated rivers had higher scores along PC1, i.e. they had a more
368 “stable” flow regime (Table 1; Fig. 2).

369

370 **3.2 Effect of flow regime compared to other environmental variables on benthic algal** 371 **and macroinvertebrate assemblages and traits**

372 In order to separate the effects of flow regime from those of other (correlated) explanatory
373 variables, regulated and unregulated sites were analyzed separately (but PC scores for flow
374 regime were calculated from the pooled dataset, and the results were later separated into
375 regulated and unregulated sites; this was done in order to ensure that characterization of flow
376 regime was comparable between regulated and unregulated sites). In unregulated rivers, flow
377 regime (characterized as PC_{hydr}1 and 2) was correlated with half of the other explanatory
378 variables, particularly geographic location, the distance to the nearest upstream lake,
379 catchment size, some water chemical variables and temperature (Table 2). This was not
380 surprising, since the flow regime of unregulated rivers is determined by catchment
381 characteristics and climate, which in turn are related to water chemistry and geographic
382 location. Likewise, more than half of the response variables were correlated with flow regime
383 (Table 2). However, due to the many correlations among flow regime and the other
384 explanatory variables (see above), deducing possibly causal relationships between flow
385 regime and responses was not possible.

386 In contrast, flow regime of the regulated rivers exhibited fewer correlations with other
387 explanatory variables (Table 2). Again, this was not surprising since the flow regime of
388 regulated rivers is tailored to human needs so that climate and geology less affect it.
389 Nevertheless, PC_{hydr}1 was also in regulated rivers correlated with latitude and temperature,
390 and PC_{hydr}2 was correlated with catchment size, % turbulent flow and stream width (Table 2).
391 However, in regulated rivers, only PC_{hydr}1 scores correlated with macroinvertebrate species
392 assemblages (reflected as NMDS1 values), as well as with LIFE scores (Table 2; Fig. 3). No
393 other correlations among PC axes and any of the response variables occurred in regulated
394 rivers. Because PC_{hydr}1 in regulated rivers correlated with latitude and temperature (Table 2),
395 this indicates that macroinvertebrate species composition and LIFE scores were affected by
396 latitude, temperature, or flow regime (if we disregard a possible effect of other variables
397 which we have not measured). The absence of other correlations among PC axes and response
398 variables in regulated rivers indicates that all other relationships that occurred in rivers with a
399 natural flow regime, were unlikely to be caused by flow regime, but by one (or several) of the
400 explanatory variables that correlated with PC_{hydr}1 or 2 (Table 2; note that data ranges were
401 comparable between regulated and unregulated rivers (Table 1)). In other words: our results
402 indicate that flow regime may have affected macroinvertebrate species composition and LIFE
403 scores, but no other structural or functional characteristics of benthic algae and
404 macroinvertebrates.

405 In order to explore this further, we computed a set of multivariate linear models, separately
406 for LIFE and NMDS1.MI, and selected the best models based on AIC. Although temperature
407 explained most of the variance in NMDS1 scores, and latitude explained most of the variance
408 in LIFE scores, PC_{hydr1} was retained in both cases (Table 3). This indicates that flow regime
409 significantly affected macroinvertebrate species assemblages, as well as LIFE scores (with
410 lower LIFE scores, indicating a macroinvertebrate assemblage that prefers lower flow, at sites
411 with a “stable” flow regime, i.e. high scores along PC_{hydr1}).

412 However, PC axes represent summarized descriptors of flow regime. Therefore, instances
413 where one or few individual components of flow regime (e.g. maximum June discharge,
414 number of high pulses, etc.) are influential may be overlooked. To explore which of the
415 explanatory variables, including each of the 78 hydrological variables, were most closely
416 related to the response variables, we calculated a correlation matrix and summarized the
417 strongest correlation coefficients (Table 4). Complete results are given in appendix (Table
418 A.4). Regulated and unregulated sites were pooled, because none of the above results
419 indicated a major effect of river regulation, the higher number of sites in the pooled dataset
420 reduced the chance of accidentally significant relationships (false positives), and the different
421 autocorrelations among explanatory variables in regulated and unregulated rivers often
422 prevented a meaningful interpretation of the results from separated datasets. We decided
423 against modelling response variables from the explanatory variables, because the high number
424 of autocorrelations greatly hampered differentiating between possibly causal and random
425 relationships. Instead, we interpreted the results of the correlation matrix against the
426 background of published information (Table 4).

427

428 **4. Discussion**

429 *Effects of river flow compared to other environmental variables*

430 Hypothesis 2, which stated that assemblages adapted to low flow conditions would occur at
431 sites with a more stable flow regime, was accepted for macroinvertebrates, but not for benthic
432 algae. Overall flow regime, characterized as principal components calculated from 78
433 hydrological variables over the five years preceding sampling, affected macroinvertebrate
434 species assemblages, reflected in NMDS and LIFE scores (Table 3). LIFE is based on
435 macroinvertebrate taxa associated with different “flow groups” (from “rapid” via “slow” to
436 “standing” and “drought resistant”), and was designed to assess changes in prevailing flow

437 regimes (Extence et al., 1999). An effect of flow regime on LIFE scores therefore simply
438 meets expectations. Although many benthic macroinvertebrate taxa can live under varying
439 flow regimes (Statzner et al. 1988), some taxa including heptageniid mayfly nymphs and
440 blackfly larvae exhibit behavioural and morphological adaptations to high current velocities
441 (Hart et al. 1991, Weissenberger et al. 1991). This likely explains the change in
442 macroinvertebrate species composition, reflected in NMDS scores, with flow regime.

443 Short-term effects of extreme events on macroinvertebrates and benthic algae are a well-
444 known phenomenon (Extence et al., 1999; Monk et al., 2008; Power et al., 2008). However,
445 even though flood scour and dewatering indeed rejuvenate riverine ecosystems,
446 macroinvertebrates and benthic algae rapidly reassemble after such events (Power et al.,
447 2013). Rapid reassembly will lead to the absence of correlations between long-term flow
448 regime and response variables. Given rapid recolonization, a relation between overall flow
449 regime and a biological response will only emerge once the species pool, from which
450 recolonization occurs, has been affected. Our results indicate that overall flow regime (as
451 characterized by PC1_{hydr}) affected the species pool of macroinvertebrates, but not of benthic
452 algae. This indicates that macroinvertebrate assemblages are more sensitive to long-term
453 overall flow regime than benthic algae. This is in accordance with earlier studies that analyzed
454 flood effects on macroinvertebrates and periphyton, which either reported that both were
455 affected (“high floods”; Danehy et al., 2012; Fuller et al., 2011; Robinson and Uehlinger,
456 2008), or neither of the two was affected (“low floods”; Tonkin and Death, 2014), or that
457 macroinvertebrates were more sensitive than periphyton (Robinson, 2012).

458 We have no evidence that overall flow regime affected benthic algal assemblages, taxon
459 richness, biomass, potential N-fixation, or indices used for ecosystem status assessment
460 (Table 2). Neither did flow regime affect macroinvertebrate taxon richness, overall density,
461 density of functional feeding groups or indices used for ecosystem status assessment (Table
462 2). This indicates that, though macroinvertebrate species identity shifted with changing flow
463 regime (along NMDS1), the exchanged taxa had similar functional feeding habits. We would
464 like to stress that these inferences are only valid for flow regimes that are within the
465 variability we experienced in our dataset (Tables 1, A.6). For example, “extreme” regulation
466 causing streambed drying did not occur at our sites, due to the climatic conditions in Norway,
467 and because of environmental flow regulations aimed at avoiding streambed drying
468 (Alfredsen et al., 2012). If regulation had caused streambed drying, consequences for biota

469 would probably have been severe (Bonada et al., 2007; Hille et al., 2014; Elias et al., 2015;
470 Verdonschot et al., 2015).

471 However, overall flow regime is a summary parameter which may overlook potential effects
472 of individual components of flow regime on river biota. We therefore also analyzed the
473 effects of each of the 78 hydrological variables which constitute flow regime, and compared
474 them with the effects of water chemistry and habitat characteristics. Although the large
475 number of autocorrelations among explanatory variables prevented relating the observed
476 differences in response variables to single explanatory variables with confidence, the
477 following inferences were possible (Table 4);

478 (1)*Macroinvertebrate and benthic algal species assemblages were more closely related to*
479 *water chemical than to hydrological variables*; benthic algal assemblages were best
480 explained by water calcium concentrations and conductivity (Tables A.4, 4); Calcium and
481 conductivity were correlated with each other, and their effect on algal assemblages is
482 probably related to the increased availability of inorganic carbon in “hard water”; a
483 relationship between benthic algal assemblages and water calcium concentrations is
484 common and has also been shown in Norway before (Schneider, 2011). Benthic algal
485 assemblages also were related to water TP concentrations (as expected; see Schneider and
486 Lindstrøm, 2011), but the correlation was weak due to the low number of sites with high
487 TP concentrations in our data. Macroinvertebrate assemblages were closest related to water
488 temperature and TOC concentrations; temperature and TOC were correlated with each
489 other, but both are well-known to affect macroinvertebrates: the effect of temperature is
490 related to species requirements with respect to growth and egg hatching (Lillehammer,
491 1987; Lillehammer et al., 1989), while TOC has multiple effects, including its use as food
492 for decomposers (Thomas, 1997).

493 (2)*flow maxima were related to algal taxon richness, and flow minima to macroinvertebrate*
494 *taxon richness; however, recovery probably is fast*; high June (i.e. three months before
495 sampling) flow maxima were (weakly but significantly) associated with low benthic algal
496 taxon richness (Tables A.4, 4); this may be explained by a short-term effect of flood scour
497 (Biggs and Smith, 2002). However, neither Biggs and Smith (2002) nor our own results
498 with respect to hydrological variables calculated from five years-flow regime (Tables 2, 4,
499 A.4) indicate long-lasting effects of flow regime on benthic algal richness patterns in
500 streams. This suggests that sufficient algae remain after flood scouring to permit rapid
501 recolonization. Benthic algal taxon richness was weakly but significantly negatively

502 correlated with water TP-concentrations; such a relationship has been found before
503 (Schneider et al., 2013b) and may be explained by the classical concept of niche theory,
504 where taxon richness decreases with increasing nutrient supply due to the exclusion of taxa
505 by superior competitors (Stevens et al., 2004; Wassen et al., 2005). Macroinvertebrate
506 taxon richness generally increased with increasing minimum discharges, and the strongest
507 relation was with May and November minimum discharges during the year before
508 sampling (Tables 4, A.4). Temporary drying of the riverbed may affect the densities of
509 benthic macroinvertebrates and hence species diversity (Clarke et al., 2010). Consequently,
510 if lower minimum discharge levels resulted in partial drying of the riverbed, then this may
511 explain the finding of lower macroinvertebrate richness where minimum discharge was
512 lowest.

513 (3)*benthic algal biomass and cover was related to water chemistry and river flow, but their*
514 *relative importance was uncertain*; epilithic Chl *a* and total algal cover were positively
515 correlated with water temperature, TOC concentrations and winter discharges, and
516 negatively with summer discharges (Tables 4, A.4). Since these variables were correlated
517 with each other, their relative importance for benthic algal biomass and cover could not be
518 deduced with confidence. Each of them may in fact be influential: temperature affects algal
519 growth (Piggott et al., 2015), which may lead to a positive relation between temperature
520 and benthic algal biomass in streams (Schneider, 2015); TOC may be beneficial by
521 preventing damage caused by ultraviolet light (Kelly et al., 2001) and by providing a
522 nutrient source that is accessible for some taxa via phosphatase (Whitton et al., 1991); high
523 winter discharges may prevent freezing and drying damage (Lind and Nilsson, 2015), and
524 high summer discharges may harm due to scouring (Francoeur and Biggs, 2006).

525 (4)*macroinvertebrate density was poorly related to water chemistry or river flow*; this is at
526 odds with earlier studies which observed higher macroinvertebrate densities at phosphorus-
527 enriched sites (Rader and Richardson, 1992; McCormick et al, 2004); we suggest that our
528 dataset contained too few clearly nutrient-enriched sites; this may have prevented the
529 detection of nutrient effects given that disturbance regime may modify macroinvertebrate
530 responses (Gafner and Robinson, 2007); in our data, the closest relation (Pearson $r = 0.47$)
531 occurred with autumn minimum discharges (high October and November minimum
532 discharges were associated with higher macroinvertebrate density; Tables 4, A.4); this may
533 be related to partial drying of the riverbed at low minimum discharges (temporary drying
534 of the riverbed affects the densities of benthic macroinvertebrates; Clarke et al. 2010).

535 (5) *we were unable to confidently establish relationships between species traits (related to*
536 *potential nitrogen fixation, grazing, filtering, degradation of CPOM and FPOM) and*
537 *water chemistry or river flow;* The abundance of N-fixing algae has earlier been shown to
538 be related to water nitrate (plus nitrite) concentrations (Stancheva et al., 2013; Gillett et al.,
539 2016), a parameter which we have not measured (only total N). We therefore cannot
540 exclude that a relation between water nitrate concentrations and the abundance of N-fixing
541 algae existed also in our dataset. Low flow minima indeed tended to decrease the number
542 of filter feeders (Tables 4, A.4), which may be explained by their dependence on a
543 minimum flow to transport food particles. However, many autocorrelations occurred
544 among hydrological variables, and – most importantly – there was also a negative
545 relationship between the number of filter feeders and the distance between the sampling
546 site and the nearest upstream lake/reservoir (Table A.4). An enhanced number of filter
547 feeders in lake outlets is a well-known phenomenon (Malmqvist and Eriksson, 1995). We
548 therefore deem a relationship between the number of filter feeders and flow minima
549 uncertain, and request further studies before conclusions may be drawn with confidence.
550 There was a weak but significant trend that more grazers and more collectors occurred at
551 high pH (Table A.4), but autocorrelations occurred with geographic position. The absence
552 of strong relationships between water chemistry, hydrological variables and
553 macroinvertebrate functional feeding groups may be related to many macroinvertebrate
554 species showing flexible feeding habits (Rawer-Jost et al., 2000), but also to the
555 overarching effect of riparian vegetation on stream food webs, via litter input (Wallace et
556 al., 1997), as well as to the manifold interactions between hydrochemistry, flow, primary
557 producers and consumers (Lamberti et al., 1991; Wallace et al., 1997) which may
558 confound straightforward relationships.

559 (6) *We found no indications that river flow affected macroinvertebrate and benthic algal*
560 *acidification indices;* both acidification indices (AIP for benthic algae and Raddum 2 for
561 macroinvertebrates) were most closely related to pH. These indices were designed to
562 reflect pH (Raddum and Fjellheim, 1984; Raddum 1999; Schneider and Lindstrøm, 2009),
563 and we therefore suggest that all other relationships among these indices and other
564 explanatory variables (Table A.4) were due to their autocorrelation with pH.

565 (7) *the LIFE index was useful for characterizing overall flow regime;* The LIFE index was
566 most closely related to latitude, but it also was correlated with overall flow regime
567 (characterized as principal components; Table 2). Across our sampling sites, highest
568 precipitation generally occurred at the southernmost sites, and precipitation changed

569 roughly linearly with latitude (www.met.no). Consequently, latitude correlated with overall
570 flow regime, and may - in our dataset - indeed be a surrogate variable for long-term flow
571 regime. The other environmental variables that were related to the LIFE index (Table A.4)
572 also were correlated with latitude (data not shown). There are several arguments which
573 together suggest that the LIFE index indeed may be useful for characterizing overall flow
574 regime (also in Norway where it previously has not been tested): (i) the LIFE index was
575 designed to assess changes in prevailing flow regimes (Extence et al., 1999), and a recent
576 adaptation of the LIFE index to New Zealand also primarily correlated with hydrological
577 variables instead of water chemistry (Greenwood et al., 2016); (ii) the LIFE index
578 correlated with PC1_{hydr}, and (iii) among 97 environmental variables in our dataset, the
579 LIFE index was most closely related to latitude, which in our dataset likely reflects overall
580 flow regime.

581

582 *Effects of river regulation*

583 Hypothesis 1, which stated that regulated sites would have a more stable flow regime than
584 unregulated sites and that this would lead to fewer macroinvertebrate and benthic algal taxa in
585 regulated than in unregulated sites, was only partly accepted. Regulated sites indeed had a
586 more stable flow regime (Table 1), but this was not associated with reduced taxon richness.
587 Neither have we found differences in macroinvertebrate and benthic algal assemblages and
588 functional traits between regulated and unregulated rivers (Table 1). The absence of
589 systematic differences in aquatic biota between regulated and unregulated sites may at first
590 sight be surprising, but is in line with results of Poff and Zimmerman (2010), who were
591 unable to develop general relationships between flow alteration and ecological response.
592 River regulation may have manifold consequences, affecting not only river flow, but also
593 water temperature, nutrient concentrations, organic matter and alkalinity/pH, among others
594 (reviewed by Gracey and Verones, 2016). These water physico-chemical variables were
595 among those that explained most of the variability in benthic algal and macroinvertebrate
596 assemblages and biomass (Table 4). To which degree and in which direction water quality
597 and quantity are affected by an individual hydropower plant depends on the location, design
598 and management of the dam/power plant, such that effects vary between sites (Gracey and
599 Verones, 2016). For example, river regulation may increase or decrease water temperature
600 (Gracey and Verones, 2016). This will lead to different responses among river biota. For
601 example, mass developments of macrophytes and benthic algae may occur downstream the

602 outlet of some but not other hydropower plants (Johansen et al., 2000). Also, the severity and
603 direction of responses in fish communities and traits to river regulation vary widely (Murchie
604 et al. 2008). The absence of systematic differences between regulated and unregulated rivers
605 therefore does not contradict observed differences between upstream and downstream
606 locations of dams (Lessard and Hayes, 2003), or before and after river regulation (Dejalon
607 and Sanchez, 1994) at specific river sites. The question is, however, whether these observed
608 differences at specific sites were caused by the changes in river flow, or by concomitant
609 changes in water physico-chemistry.

610 Our results indicate that overall flow regime affected macroinvertebrate assemblages
611 (reflected in NMDS and LIFE scores), but the difference in flow regime between regulated
612 and unregulated sites was not sufficiently large to be reflected in macroinvertebrate
613 assemblages. The results also indicated that many of our response variables primarily respond
614 to water physico-chemical variables (Table 4). Together with the fact that river regulation
615 may affect both flow regime and water physico-chemistry to various degrees, this may
616 explain the absence of consistent differences between regulated and unregulated sites. It also
617 explains the observed wide variations in the severity and direction of biological responses in
618 regulated rivers (Murchie et al., 2008). Our data carefully suggest that changes in water
619 physico-chemistry caused by river regulation may be equally important for benthic algae and
620 macroinvertebrates than changes in river flow. Understanding these relationships is essential
621 for improvement of river management practices, and for planning remediation measures to
622 minimize effects of river regulation on aquatic biota. In addition, using data on river flow for
623 relating observed changes in riverine biota to river regulation may lead to misleading results
624 when concomitant changes in water physico-chemical parameters are not taken into account.

625 We observed no differences between regulated and unregulated rivers in any of the indices
626 used for ecological status assessment (Raddum 2 and AIP for acidification, ASPT and PIT for
627 eutrophication/organic pollution; Table 1). Both acidification indices responded closely to pH,
628 irrespective of river regulation (a similar analysis for PIT and ASPT was not possible because
629 too few eutrophic sites occurred in our dataset, preventing a meaningful interpretation of
630 correlations). Consequently, our results (i) give no reason for defining “good ecological
631 potential” in regulated rivers differently than “good ecological status” in unregulated rivers,
632 and (ii) suggest that the existing assessment systems for macroinvertebrates and benthic algae
633 with respect to acidification and eutrophication (Raddum 2, AIP, ASPT, PIT) may also be
634 applicable in regulated rivers.

635 Our results indicate that long-term modification of flow regime towards more “stable”
636 conditions (as characterized by PC1_{hydr}) may lead to changes in macroinvertebrate
637 assemblages, which are reflected in the LIFE index (Extence et al., 1999). The LIFE index
638 therefore seems a suitable response parameter for monitoring long-term changes in flow
639 regime (time series data).

640

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647

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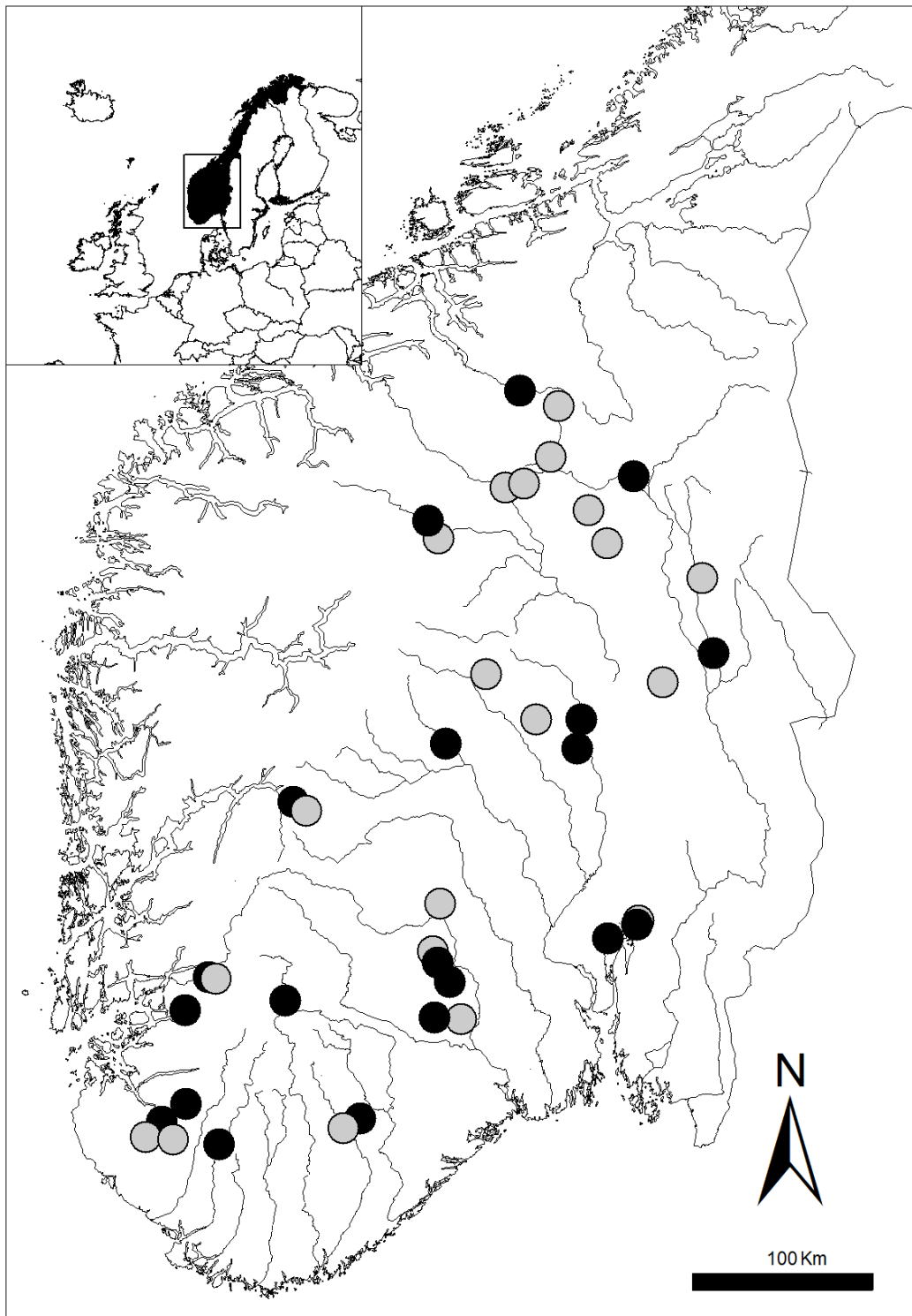
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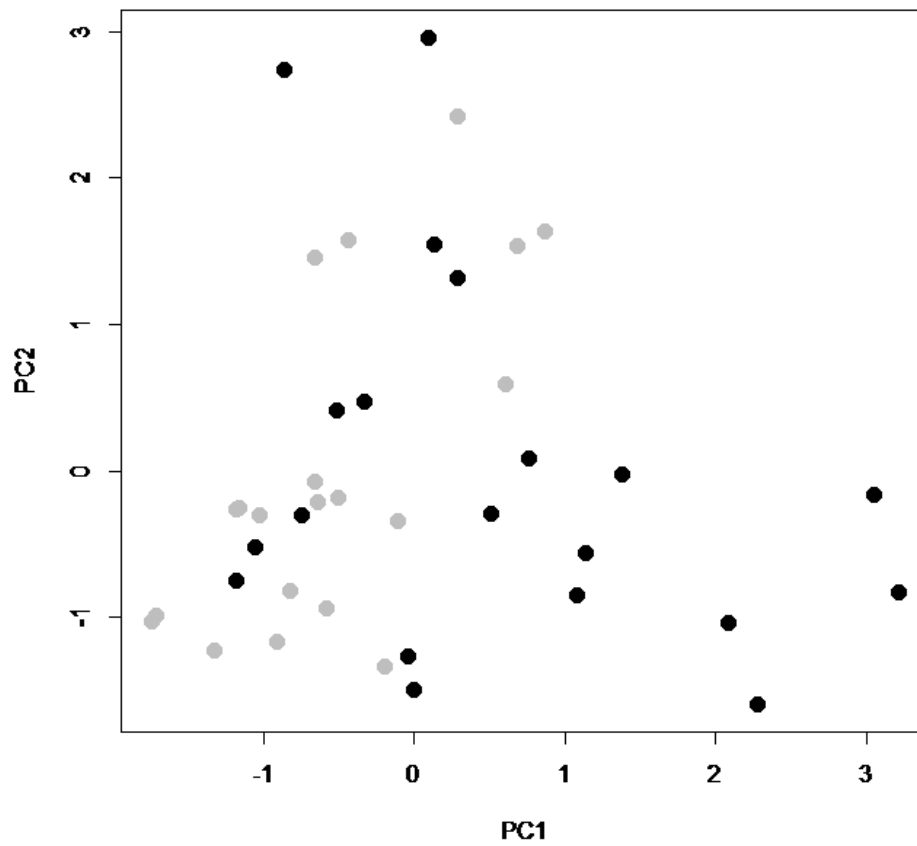
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882 **Fig. 1:** map of 40 sampling sites in Norway; \hat{o} = regulated (modified flow regime), $\hat{o} =$
883 unregulated (natural flow regime)

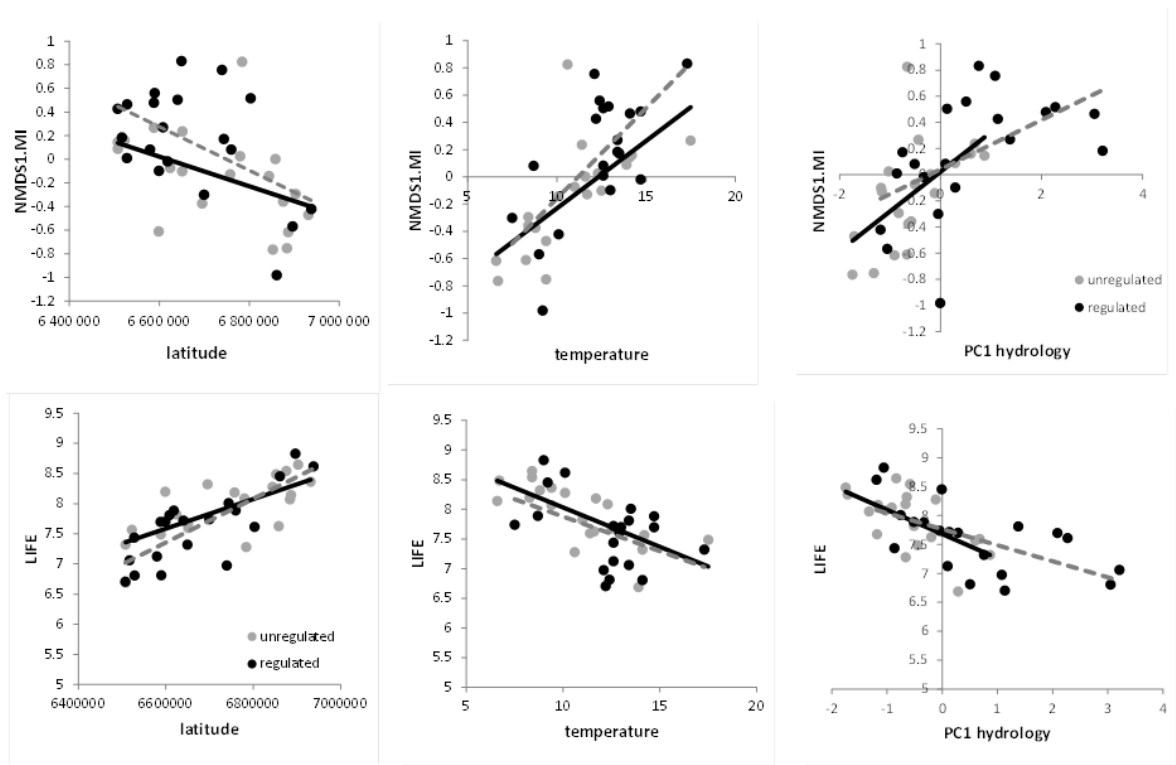
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886 **Fig. 2.** PCA of 78 hydrological variables (Table 1) characterizing river flow at regulated (\hat{o})

887 and unregulated (\hat{o}) river sites



888

889 **Fig. 3.** Scatter plots of response and explanatory variables that were significantly correlated
 890 with flow regime at both regulated ($\hat{\circ}$) and unregulated ($\hat{\circ}$) river sites (Table 2). NMDS.MI =
 891 non-metric multidimensional scaling scores (along axes 1) for macroinvertebrates, LIFE =
 892 LIFE index for macroinvertebrates.

893

894

895 **Table headings**

896

897 **Table 1.** Summary statistics for regulated and unregulated sites, and p-values for differences
898 between groups (t-test). Significant differences are marked in bold. Underlined p-values were
899 calculated from corrected values of the response variables, i.e. which were corrected for
900 differences in explanatory variables other than flow regime (by using the models given in
901 Table A.3).

explanatory variables	unregulated					regulated					p-value for difference between groups
	N	Mean	Std.Dev.	5 percentile	95 percentile	N	Mean	Std.Dev.	5 percentile	95 percentile	p
mean discharge											
<i>average 5 years</i>											
log (x+1) mean discharge january relative to mean (%)	20	1.38	0.24	1.01	1.87	20	1.69	0.30	1.24	2.18	0.001
log (x+1) mean discharge february relative to mean (%)	20	1.21	0.22	0.83	1.61	20	1.64	0.32	1.19	2.15	0.000
log (x+1) mean discharge march relative to mean (%)	20	1.42	0.27	1.04	1.84	20	1.73	0.24	1.34	2.10	0.000
mean discharge april relative to mean (%)	20	98.33	61.55	27.61	230.16	20	107.55	48.56	41.85	206.69	0.602
mean discharge may relative to mean (%)	20	222.8	81.1	106.1	357.1	20	160.4	66.8	68.1	280.3	0.012
mean discharge june relative to mean (%)	20	184.76	89.77	50.89	323.71	20	132.05	72.65	44.78	275.37	0.048
mean discharge july relative to mean (%)	20	149.83	62.99	67.36	274.95	20	120.22	52.44	43.61	222.25	0.114
mean discharge august relative to mean (%)	20	138.74	38.08	69.39	195.99	20	123.08	37.10	54.12	184.15	0.196
mean discharge september relative to mean (%)	20	116.33	20.62	72.94	144.91	20	119.39	37.55	72.57	204.09	0.751
mean discharge october relative to mean (%)	20	92.69	30.86	50.87	150.57	20	99.04	31.42	42.98	153.02	0.523
log (x+1) mean discharge november relative to mean (%)	20	2.13	0.84	0.57	3.34	20	1.55	0.71	0.41	2.60	0.023
log (x+1) mean discharge december relative to mean (%)	20	1.54	0.22	1.14	1.91	20	1.77	0.22	1.39	2.15	0.002
<i>one year before sampling</i>											
log (x+1) mean discharge january 1 yrs relative to mean	20	0.11	0.08	0.03	0.30	20	0.19	0.11	0.04	0.40	0.009
log (x+1) mean discharge february 1 yrs relative to mean	20	0.05	0.02	0.01	0.09	20	0.16	0.13	0.01	0.39	0.001
log (x+1) mean discharge march 1 yrs relative to mean	20	0.04	0.02	0.00	0.06	20	0.14	0.13	0.01	0.43	0.001
log (x+1) mean discharge april 1 yrs relative to mean	20	0.17	0.14	0.03	0.45	20	0.26	0.11	0.08	0.42	0.035
mean discharge may 1 yrs relative to mean	20	3.82	1.33	1.85	5.91	20	2.66	1.45	0.57	5.16	0.012
mean discharge june 1 yrs relative to mean	20	2.13	0.84	0.57	3.34	20	1.55	0.71	0.41	2.60	0.023
mean discharge july 1 yrs relative to mean	20	0.85	0.49	0.24	1.83	20	0.93	0.56	0.31	2.09	0.566
mean discharge august 1 yrs relative to mean	20	1.14	0.47	0.40	2.07	20	1.04	0.47	0.34	1.82	0.497
mean discharge september 1 yrs relative to mean	20	0.94	0.40	0.53	1.78	20	0.95	0.50	0.26	1.93	0.942
mean discharge october 1 yrs relative to mean	20	0.87	0.46	0.32	1.82	20	1.03	0.54	0.31	2.21	0.335
log (x+1) mean discharge november 1 yrs relative to mean	20	0.28	0.17	0.08	0.58	20	0.34	0.14	0.11	0.60	0.229
log (x+1) mean discharge december 1 yrs relative to mean	20	0.12	0.04	0.04	0.18	20	0.20	0.10	0.09	0.39	0.001
magnitude of extremes											
max relative to mean (%)	20	1299.2	298.7	796.6	1774.9	20	1234.1	813.1	275.4	2660.9	0.739
min relative to mean (%)	20	5.1	3.7	0.2	12.3	20	6.8	6.5	0.0	19.9	0.312
95 perc. relative to mean (%)	20	346.8	41.9	270.1	422.1	20	282.0	72.8	164.5	392.2	0.001
log (x+1) 5 perc. relative to mean (%)	20	0.9	0.2	0.6	1.2	20	1.2	0.3	0.7	1.7	0.004
difference min-max relative to mean (%)	20	1294.2	298.6	784.1	1771.6	20	1227.3	816.1	256.4	2657.4	0.733
difference 95-5 percentile relative to mean (%)	20	338.4	44.8	254.7	417.5	20	263.2	83.7	117.5	382.8	0.001
difference 99-1 percentile relative to mean (%)	20	635.6	107.3	463.8	807.9	20	492.4	205.3	156.1	793.2	0.009
75 perc. relative to mean (%)	20	129.8	14.0	109.0	155.9	20	128.7	24.2	102.8	178.8	0.861
25 perc. relative to mean (%)	20	20.2	6.4	8.8	31.5	20	35.7	20.0	16.0	73.5	0.002
average yearly max relative to mean discharge (%)	20	910.4	148.5	638.8	1125.3	20	796.1	472.9	218.4	1777.9	0.309
coefficient of variation yearly max	20	0.54	0.06	0.46	0.63	20	0.52	0.16	0.20	0.74	0.529
average yearly min relative to mean discharge (%)	20	9.01	4.16	3.96	17.59	20	13.99	9.91	2.78	34.62	0.045
coefficient of variation yearly min	20	0.44	0.21	0.19	0.88	20	0.52	0.31	0.10	1.17	0.326
7 day max 5 years relative to mean discharge	20	8.59	2.30	5.27	12.40	20	6.41	2.93	2.08	10.78	0.013
7 day min 5 years relative to mean discharge	20	0.06	0.04	0.00	0.12	20	0.09	0.07	0.01	0.23	0.068
log (x+1) max discharge january 1 yrs relative to annual mean	20	0.22	0.23	0.03	0.75	20	0.30	0.21	0.06	0.77	0.265
log (x+1) max discharge february 1 yrs relative to annual mean	20	0.07	0.03	0.01	0.13	20	0.20	0.15	0.02	0.47	0.000
log (x+1) max discharge march 1 yrs relative to annual mean	20	0.04	0.02	0.00	0.07	20	0.17	0.15	0.02	0.46	0.000
log (x+1) max discharge april 1 yrs relative to annual mean	20	0.37	0.31	0.06	0.91	20	0.50	0.24	0.15	0.93	0.153
max discharge may 1 yrs relative to annual mean	20	10.52	3.68	4.38	16.84	20	9.21	6.81	1.09	20.79	0.468
max discharge june 1 yrs relative to annual mean	20	5.50	2.37	1.69	9.12	20	3.67	2.02	1.06	7.08	0.012
max discharge july 1 yrs relative to annual mean	20	2.05	0.76	0.58	3.19	20	1.96	1.21	0.50	4.74	0.782
max discharge august 1 yrs relative to annual mean	20	3.19	1.52	0.98	6.06	20	2.78	1.40	0.79	5.21	0.378
max discharge september 1 yrs relative to annual mean	20	2.29	1.72	1.00	6.51	20	2.44	2.17	0.85	8.38	0.806
max discharge october 1 yrs relative to annual mean	20	2.21	1.46	0.86	4.92	20	2.46	2.26	0.50	8.34	0.681
log (x+1) max discharge november 1 yrs relative to annual mean	20	0.45	0.21	0.13	1.00	20	0.52	0.26	0.16	1.03	0.456
log (x+1) max discharge december 1 yrs relative to annual mean	20	0.24	0.18	0.06	0.69	20	0.35	0.24	0.11	0.86	0.105
log (x+1) min discharge january 1 yrs relative to annual mean	20	0.05	0.03	0.01	0.10	20	0.12	0.11	0.00	0.34	0.009
log (x+1) min discharge february 1 yrs relative to annual mean	20	0.04	0.02	0.00	0.06	20	0.12	0.11	0.01	0.35	0.003
log (x+1) min discharge march 1 yrs relative to annual mean	20	0.03	0.02	0.00	0.06	20	0.11	0.11	0.01	0.38	0.002
log (x+1) min discharge april 1 yrs relative to annual mean	20	0.03	0.02	0.00	0.05	20	0.07	0.06	0.01	0.18	0.002
log (x+1) min discharge may 1 yrs relative to annual mean	20	0.14	0.09	0.03	0.31	20	0.16	0.09	0.04	0.32	0.414
min discharge june 1 yrs relative to annual mean	20	0.97	0.52	0.21	1.94	20	0.74	0.50	0.09	1.63	0.164
log (x+1) min discharge july 1 yrs relative to annual mean	20	0.14	0.10	0.02	0.33	20	0.15	0.11	0.02	0.38	0.646
log (x+1) min discharge august 1 yrs relative to annual mean	20	0.13	0.10	0.03	0.29	20	0.15	0.11	0.02	0.37	0.575
min discharge september 1 yrs relative to annual mean	20	0.46	0.20	0.16	0.84	20	0.41	0.26	0.08	0.87	0.500
log (x+1) min discharge october 1 yrs relative to annual mean	20	0.14	0.06	0.06	0.26	20	0.16	0.09	0.05	0.33	0.505
log (x+1) min discharge november 1 yrs relative to annual mean	20	0.15	0.07	0.06	0.29	20	0.16	0.09	0.04	0.31	0.675
min discharge december 1 yrs relative to annual mean	20	0.19	0.09	0.04	0.32	20	0.38	0.30	0.05	1.02	0.010
timing of extremes											
Julian day of max 1 year before sampling	20	166	63.0	134	315	20	160	49.3	136	293	0.709
days between sampling and last maximum	20	152	71.4	92	299	20	120	69.8	95	317	0.608
Julian day of min 1 year before sampling	20	125	70.7	74	289	20	119	83.4	15	311	0.817
average Julian day maximum	20	152	45.1	73	218	20	175	72.7	39	307	0.236
average Julian day minimum	20	69	20.5	26	97	20	74	63.6	6	204	0.743
month with highest discharge	20	6	1.9	4	11	20	5	2.2	1	10	0.358
frequency and duration of high pulses (high pulse is > 0.9 percentile)											
number of days with high pulses 1 year before sampling	20	40	7.3	28	49	20	39	10.3	19	56	0.699
number of high pulses 1 year before sampling	20	8	4.7	3	18	20	10	5.8	4	22	0.368
total number of high pulses in 5 years	20	44	22.9	23	81	20	46	19.9	21	87	0.678
average duration of high pulses (days)	20	3	1.2	2	6	20	3	1.3	1	6	0.846
rate of change											
log (x+1) maximum rising limb relative to average discharge 5 years	20	0.88	0.13	0.67	1.05	20	0.82	0.34	0.25	1.33	0.454
- log (sqrt of quadrat of minimum falling limb relative to average discharge 5 years)	20	-0.72	0.18	-0.01	-0.36	20	-0.66	0.43	-0.37	0.00	0.580
average rising limb relative to average discharge 5 years	20	0.37	0.15	0.20	0.68	20	0.31	0.21	0.07	0.80	0.284
average falling limb relative to average discharge 5 years	20	-0.19	0.08	-0.36	-0.11	20	-0.19	0.11	-0.45	-0.06	0.903
base flow index											
BFI 5 years	20	0.519	0.1	0.32	0.70	20	0.579	0.2	0.25	0.85	0.198
BFI 1 years before sampling	20	0.517	0.1	0.31	0.69	20	0.582	0.2	0.22	0.87	0.206
Principal components of hydrological variables											
PC1 hydr	20	-0.56	1.3	-1.73	0.77	20	0.56	1.3	-1.12	3.13	0.002
PC2 hydr	20	0.01	1.1	-1.28	2.03	20	-0.01	1.3	-1.54	2.85	0.978
Response variables											
<i>species assemblages</i>											
NMDS1 algae	19	0.06	0.56	-0.61	1.93	20	-0.06	0.61	-1.56	0.52	0.517
NMDS2 algae	19	-0.03	0.43	-0.86	1.13	20	0.03	0.40	-0.75	0.53	0.626
number of taxa algae	20	17.58	6.95	1.50	25.75	20	18.40	5.30	9.00	26.75	0.675
NMDS1 MI	20	-0.15	0.40	-0.76	0.65	20	0.15	0.46	-0.58	0.79	0.380
NMDS2 MI	20	-0.01	0.35	-0.42	0.81	20	0.01	0.47	-0.66	0.84	0.820
number of taxa MI	20	10.82	3.89	4.75	17.00	20	14.01	7.11	4.05	26.50	0.428
<i>abundance</i>											
log (x+1) chl a µg/cm²	20	0.36	0.17	0.05	0.69	20	0.46	0.23	0.12	0.83	0.657
log (x+1) % cover algae	20	1.02	0.59	0.06	1.91	20	1.07	0.56	0.30	1.91	0.471
log density MI [ind/m²]	20	1.82	0.36	1.13	2.34	20	1.98	0.50	0.97	2.71	0.255
<i>ecosystem processes</i>											
log (x+1) % cyanobacteria with heterocysts	20	0.27	0.58	0.00	1.90	20	0.19	0.26	0.00	0.77	0.550

903

904 **Table 2.** Correlations (Pearson r) among flow regime (calculated as principal components
905 (PC_{hydr}) from 78 hydrological variables) and other explanatory variables as well as response
906 variables, separately for regulated and unregulated sites. Variables were transformed as
907 described in Table 1. Significant (Pearson; $p < 0.05$) correlations with PC axes are marked in
908 bold. Note that PC_{hydr} axes were calculated from the pooled dataset, and the results were later

909 separated into regulated and unregulated sites. This was done in order to ensure that
 910 characterization of flow regime was comparable between regulated and unregulated sites.

	unregulated		regulated	
	PC1 hydr	PC2 hydr	PC1 hydr	PC2 hydr
<i>explanatory variables other than flow regime</i>				
longitude (east; UTM 32)	-0.211	-0.516	-0.125	-0.313
latitude (north; UTM 32)	-0.663	-0.876	-0.495	-0.434
dist. to lake/reservoir upstream	-0.498	-0.508	-0.390	-0.123
catchment size	-0.496	-0.507	-0.206	-0.585
altitude (m asl)	-0.412	-0.644	-0.197	-0.295
Shading (%)	0.302	0.499	-0.420	0.372
Tot-P/L [$\mu\text{g P/l}$]	-0.483	-0.262	-0.031	0.060
Tot-N/L [$\mu\text{g N/l}$]	0.662	0.792	0.075	0.331
TOC [mg C/l]	0.478	0.565	0.256	0.401
Ca [mg/l]	-0.419	-0.358	-0.409	-0.016
conductivity ($\mu\text{s/cm}$)	-0.146	-0.039	-0.323	0.061
temperature (degree C)	0.531	0.631	0.460	0.216
pH	-0.606	-0.574	-0.436	0.057
% turbulent flow	-0.147	-0.287	-0.222	0.490
average depth (m)	-0.106	-0.083	0.326	-0.209
width (m)	-0.185	-0.215	0.217	-0.602
sediment PC1	0.045	0.144	0.119	0.268
sediment PC2	-0.333	-0.378	0.397	-0.208
<i>response variables</i>				
<i>species assemblages</i>				
NMDS1 algae	-0.352	-0.409	0.024	-0.018
NMDS2 algae	0.258	0.149	0.252	-0.093
number of taxa algae	0.232	0.099	0.114	0.073
NMDS1 MI	0.571	0.475	0.536	0.075
NMDS2 MI	0.322	0.463	0.356	-0.061
number of taxa MI	0.326	-0.118	0.301	0.000
<i>abundance/biomass</i>				
Chl a $\mu\text{g/cm}^2$	0.558	0.372	0.199	0.403
% cover algae	0.561	0.458	0.211	0.287
density MI [ind/m^2]	-0.050	-0.495	0.182	0.024
<i>ecosystem functions</i>				
% cyanobacteria with heterocysts	0.597	0.617	0.219	0.178
number of grazers / m^2	-0.214	-0.538	-0.006	0.069
number of shredders / m^2	0.285	-0.001	0.044	-0.208
number of filter feeders / m^2	0.177	-0.206	0.443	-0.092
number of gatherers/collectors / m^2	-0.455	-0.741	-0.321	-0.200
<i>ecosystem assessment</i>				
AIP	-0.603	-0.641	-0.392	-0.021
Raddum 2	-0.527	-0.599	-0.236	-0.090
PIT	-0.345	-0.518	-0.099	0.174
ASPT	-0.141	-0.459	0.105	-0.162
LIFE	-0.616	-0.680	-0.607	-0.177

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913 **Table 3.** Multivariate linear models for NMDS1.MI and LIFE (interactions were tested, but
 914 not significant)

formula	Adjusted R2		F-statistic	p
NMDS1.MI = -1.06 + 0.09*temperature + 0.12*PChydr1	0.5545		25.28 on 2 and 37 DF	1.20E-07
Analysis of Variance	sum of squares	mean squares	F value	P
temperature	3.9305	3.93	43.9016	8.98E-08
PC1hydr	0.5953	0.60	6.6496	0.01403
Residuals	3.3126	0.09		

formula	Adjusted R2		F-statistic	p
LIFE = -8.05 + 2.360e-06*latitude - 0.146*PC1hydr	0.6151		32.17 on 2 and 37 DF	8.05E-09
Analysis of Variance	sum of squares	mean squares	F value	P
latitude	7.1541	7.15	57.7778	4.55E-09
PC1hydr	0.8114	0.81	6.5529	0.01469
Residuals	4.5814	0.12		

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917 **Table 4.** Summary of correlation matrix between 97 explanatory variables, and the response
 918 variables; only strong correlations (Pearson $r > 0.5$ or < -0.5) are listed; + indicates positive, -
 919 negative correlations, q = discharge, MI = macroinvertebrates, CPOM = coarse particulate
 920 organic matter, FPOM = fine particulate organic matter; TP = total phosphorus; PIT and
 921 ASPT indices were excluded from this analysis because there occurred too few
 922 eutrophic/polluted sites, which prevented a meaningful interpretation of the results.

	response	calculated as	best explained by	interpretation
assemblages	algal species assemblage	NMDS 1 and 2	Ca, conductivity	algal species assemblages were mainly related to water hardness/alkalinity
	algal species richness	number of algal taxa	no correlations with $r > 0.5$, but weak correlations with TP (-) and maximum June q (-)	high water TP and high maximum June discharges (i.e. 3 months before sampling) slightly decreased algal taxon richness
	MI species assemblage	NMDS 1 and 2	longitude, latitude, TN, TOC, temperature, pH, average discharges (particularly in winter and June/July/August), min q June and November	the strongest correlations occurred with temperature and TOC, and most other variables were correlated with these; it is therefore likely that macroinvertebrate species assemblages were mainly affected by temperature and TOC
	MI species richness	number of MI taxa	5- and 25 percentile of discharge (+), 7-day min q (+), min q May and November (+)	strongest relation with May and November minimum discharges during the year before sampling; fewer macroinvertebrate species occurred in streams with low May and November minimum discharges
biomass	epilithic algal biomass	epilithic Chl a	TOC (+), mean q June (-), mean and max q November (+)	these variables were correlated with each other, and their relative importance for algal biomass is uncertain; TOC may be beneficial because many algae may use organic P via phosphatase; high summer discharges may have a negative effect due to scouring, high winter discharges (before snow falls) may be beneficial because they prevent freezing damage
	total algal cover	% algal cover	temperature (+), June and July discharges (-)	these variables were correlated with each other; high summer discharges may have a negative effect due to scouring, temperature may increase algal growth
	MI density	number of MI individuals /m ²	no correlations with $r > 0.5$, but weak correlations with October and November minimum q (+)	high autumn discharges slightly increased MI abundance; this may be due to less drying of the river bed
ecosystem functions	potential N-fixation	% cover of cyanobacteria having heterocysts	Julian day of max q (+), month with highest q (+), max q January (+)	autocorrelations occurred with geographic location, temperature and pH, which in turn may be related to nitrogen deposition and nitrogen cycling; we were unable to find arguments for causal relationships between river flow and the abundance of cyanobacteria having heterocysts
	grazing	number of grazers /m ²	longitude (+)	there also occurred a weaker but significant relation with pH (which was correlated with longitude); many grazers, e.g. snails, tend to be acid sensitive; we were unable to separate a possible effect of longitude from an effect of pH; we have no evidence for an effect of river flow characteristics
	degradation of CPOM	number of shredders /m ²	no correlations with $r > 0.5$	the number of shredders was no straightforward response to any of the measured variables; we have no evidence for an effect of river flow characteristics
	degradation of FPOM	number of collectors /m ²	longitude (+), latitude (+), pH (+), mean q January, March and November (-), max q January and November (-), mean q June (+)	strongest relation occurred with latitude, then with longitude and pH; climate (which changes with geographic position) and pH seemed to be more influential than river flow characteristics
assessment	filtering	number of filter feeders /m ²	25 percentile discharge (+)	there occurred several autocorrelations; the number of filter feeders was also negatively related to the distance between the sampling site and the nearest lake/reservoir upstream; a higher number of filter feeders at lake outlets is well-known; flow minima may reduce the number of filter feeders, but more data are needed before confident conclusions may be drawn;
	acid sensitivity of algal assemblage	AIP	longitude, latitude, Ca, conductivity, pH (all +), mean winter discharges (-), mean June discharge (+)	strongest relation occurred with pH, all other variables were correlated with pH; most likely pH was causal; we have no evidence for an effect of river flow characteristics
	acid sensitivity of MI assemblage	Raddum 2	longitude, latitude, pH (all +), winter discharge (-), may discharge (+)	strongest relation occurred with pH, all other variables were correlated with pH; most likely pH was causal; we have no evidence for an effect of river flow characteristics
	flow preference of MI assemblage	LIFE	latitude (+), pH (+), summer discharges (+), TOC (-), temp (-), winter discharges (-)	strongest relation occurred with latitude; latitude was correlated with overall flow regime (PC1 hydrology, Table 3); most likely, overall flow regime was influential

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924 **Appendix**

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926 **Table A.1.** List of sampling sites.

NVE number	name	regu- lated since	east (UTM32)	north (UTM32)	average discharge (m ³) (Sept. 2008 - Aug. 2013)
2.129	Dølplass	1916	575519	6896441	24.79
2.267	Mistra Bru		618518	6844041	13.31
2.268	Akslen		471000	6852350	26.50
2.303	Dombås		505319	6883891	10.29
2.32	Atnasjø		564319	6858291	11.38
2.434	Ofossen	1979	463919	6861292	55.79
2.439	Kvarstadseter		601818	6784141	9.19
2.479	Li Bru		552376	6875695	4.04
2.592	Fokstua		515128	6886690	0.71
2.611	Storsjøen ndf. -Øra	1940	628518	6803191	99.37
6.1	Gryta		600551	6651559	0.15
6.9	Maridalsvatn ndf.	1956	599750	6649300	3.22
8.2	Bjørnegårdsvingen	1968	584400	6640500	3.90
12.137	Gjærdeslåtten	1957	485118	6739392	23.62
12.2	Kolbjørnshus	1988	558318	6743592	24.04
12.207	Vinde-elv		504069	6779692	5.77
12.7	Etna		533918	6757592	11.35
12.8	Grønvold bru	1988	558918	6759891	8.68
16.1	Omnesfoss	1958	499618	6608170	24.46
16.128	Austbygdåi		490345	6650892	9.34
16.132	Gjuvå		488518	6624192	1.18
16.155	Sønnlandsvatn	1986	492020	6618490	4.32
16.193	Hørte		507618	6588192	4.77
16.51	Hagadrag	1944	492895	6588165	23.81
19.72	Jørundland	1963	456850	6528550	12.01
20.2	Austenå		448084	6522544	10.26
21.21	Hoslemo	1918	409604	6589839	5.59
25.6	Homstølvatn ndf.	1925	380400	6507550	1.08
27.13	Maudal	1942	347768	6516793	4.44
27.15	Austrumdal		339468	6507943	5.55
27.16	Bjordal		354718	6507793	10.65
30.8	Øvstabøstøl	1986	360100	6527850	1.38
35.2	Hauge bru	1981	354868	6579542	5.72
36.31	Kvilldal	1985	365918	6598992	0.79
36.32	Lauvastøl		370168	6598600	1.92
50.11	Høel	1968	404069	6699542	6.83
50.13	Bjoreio		411569	6695392	10.68
109.2	Grensehølen	1973	508200	6937900	29.30
109.21	Svoni		528519	6902891	3.39
109.9	Risefoss		530519	6931291	17.99

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931 **Table A.2.** PCA for sediment composition, calculated from the averaged values per site;
 932 significant correlations with PC axes are marked in bold.

Importance of components	PC1	PC2	PC3
Eigenvalue	2.472	1.958	1.205
Proportion Explained	0.309	0.245	0.151
Cumulative Proportion	0.309	0.554	0.704
PC scores	PC1	PC2	PC3
% bolders (>20cm)	1.458	-0.160	0.063
% cobbles (6-20cm)	-1.039	-0.623	-0.444
log (x+1) % gravel (2-6cm)	-1.264	0.165	-0.007
% fine gravel (2mm-2cm)	-0.233	1.222	0.243
log (x+1) % sand (0.1 mm-2mm)	-0.077	1.275	0.068
log (x+1) sediment cover CPOM (> 1mm)	0.020	0.843	-0.465
log (x+1) sediment cover FPOM (<1mm)	0.221	-0.029	1.094
log (x+1) % cover bryophytes	0.738	0.226	-0.992

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939 **Table A.3.** Regulated sites differed from unregulated sites in catchment size, altitude, TN and
 940 TOC (Table 2). Altitude, TN and TOC also correlated with each other. In order to enable
 941 unbiased comparisons between regulated and unregulated sites, the values of the response
 942 variables were corrected for these differences. The correction was done based on multivariate
 943 linear models which were computed using the MASS package in R, with forward entering of
 944 variables and model selection based on AIC. All models were significant at $p < 0.05$.

model used for correction of response variable	Adjusted R²
NMDS1.MI=-0.7968+1.5874*TOC	0.486
n.taxa.MI=7.7134+0.024*TN	0.128
Chla=0.11017+0.59898*TOC	0.311
perc.cover.algae=0.4087+1.27*TOC	0.179
n.collectors=0.4954+0.3588*catchm.size-0.941*TOC	0.191
PIT=3.9167+0.015*TN	0.169
LIFE=8.6196-1.7053*TOC	0.343

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951 **Table A.4.** Correlation matrix among explanatory and response variables; regulated and
 952 unregulated sites were pooled; correlations marked in red were significant (Pearson; $p < 0.05$),
 953 correlations additionally shimmered in red were strong (Pearson $r > 0.5$ or < -0.5).

Variable	NMDS1 algae	NMDS2 algae	number of taxa algae	NMDS1 MI	NMDS2 MI	number of taxa MI	log (x+1) chl a $\mu\text{g}/\text{cm}^2$	log (x+1) % cover algae	log density MI [ind/m ²]	log (x+1) % cyanobacteria with heterocysts	log (x+1) number of grazers	log (x+1) number of shredders	log (x+1) number of filter feeders	log (x+1) number of gatherers/collectors	AIP	Radium 226	PIT site	ASPT	LIFE
east	0.242	-0.373	-0.153	0.127	-0.670	0.460	-0.128	-0.165	0.387	-0.385	0.548	0.445	0.105	0.630	0.611	0.567	0.441	0.500	0.398
north	0.230	-0.425	-0.227	-0.525	-0.411	-0.039	-0.489	-0.463	0.175	-0.457	0.330	0.171	-0.186	0.731	0.663	0.560	0.185	0.260	0.755
log (x+1) distance to nearest lake/reservoir upstream (km)	0.001	-0.311	-0.133	-0.311	-0.187	-0.083	-0.303	-0.211	-0.007	-0.403	0.129	-0.087	-0.377	0.408	0.400	0.423	0.110	0.132	0.462
log catchment size (km ²)	0.133	0.073	-0.051	0.019	-0.150	0.103	-0.164	0.034	0.111	-0.160	0.092	0.184	-0.026	0.355	0.132	0.206	0.072	0.172	0.159
altitude (m aasl)	-0.056	-0.118	-0.062	-0.395	0.166	-0.280	-0.296	-0.360	0.004	-0.260	-0.038	-0.157	-0.122	0.279	0.085	0.195	-0.223	0.038	0.323
Shading	-0.221	-0.087	-0.171	-0.056	-0.094	-0.013	0.137	-0.003	-0.032	-0.003	0.031	0.167	-0.035	-0.130	-0.056	-0.192	-0.158	-0.006	0.023
log (x+1) Tot-P [µg P/l]	0.307	0.048	-0.241	-0.260	-0.124	-0.102	-0.231	-0.239	-0.144	-0.100	-0.065	0.009	-0.095	0.014	0.108	0.119	0.170	-0.049	0.230
Tot-N [µg N/l]	-0.082	-0.084	-0.043	0.582	-0.061	0.387	0.364	0.345	0.192	0.283	0.196	0.258	0.261	-0.286	-0.113	-0.250	0.437	0.012	-0.440
log (x+1) TOC [mg C/l]	-0.067	0.178	0.152	0.707	0.015	0.573	0.447	0.167	0.299	0.086	0.263	0.293	-0.313	-0.276	-0.238	0.146	0.308	-0.009	-0.609
log (x+1) Ca/ICP [mg/l]	0.019	-0.558	-0.250	-0.065	-0.490	0.317	-0.126	-0.142	0.332	-0.353	0.451	0.217	0.038	0.491	0.735	0.465	0.663	0.289	0.476
log conductivity	-0.049	-0.576	-0.239	0.050	-0.416	0.313	-0.054	-0.080	0.314	-0.179	0.399	0.242	0.054	0.621	0.339	0.668	0.252	0.296	
temperature	0.008	0.292	0.228	0.708	-0.044	0.299	0.410	0.501	0.102	0.334	0.009	0.183	0.243	-0.413	-0.338	-0.365	-0.045	-0.056	-0.818
pH	0.325	-0.485	0.022	-0.136	-0.599	0.318	-0.206	-0.099	0.291	-0.113	0.500	0.122	0.007	0.687	0.940	0.694	0.545	0.185	0.547
% turbulent flow	-0.121	0.017	-0.096	-0.426	-0.127	0.076	-0.042	0.045	-0.034	0.134	0.041	-0.113	0.073	0.100	0.136	0.013	0.199	0.339	
average depth (m)	0.129	0.124	0.030	0.251	0.382	-0.020	0.101	0.090	-0.171	0.144	-0.238	-0.099	0.046	-0.136	-0.272	-0.210	0.155	-0.159	-0.460
width (m)	0.195	-0.031	0.141	0.102	0.213	0.079	-0.338	0.043	0.011	-0.037	-0.026	0.021	0.038	0.096	-0.044	0.039	-0.058	-0.117	0.011
sediment PC1	0.227	0.132	0.127	0.155	0.297	-0.061	0.126	0.190	-0.074	0.271	-0.138	-0.165	0.017	-0.169	-0.262	-0.204	0.025	-0.279	-0.407
sediment PC2	-0.053	-0.107	-0.003	0.129	0.243	0.142	-0.086	-0.228	0.211	-0.265	0.098	0.179	0.132	0.087	-0.028	-0.123	-0.079	0.063	-0.121
log (x+1) mean discharge january relative to mean (%)	-0.225	0.241	0.264	0.495	0.585	0.178	0.348	0.340	0.013	0.405	-0.227	-0.030	0.297	-0.528	-0.847	-0.516	-0.144	-0.243	-0.678
log (x+1) mean discharge february relative to mean (%)	-0.188	0.228	0.245	0.481	0.509	0.213	0.284	0.270	0.092	0.318	-0.159	-0.021	0.340	-0.395	-0.486	-0.170	-0.158	-0.180	-0.608
log (x+1) mean discharge march relative to mean (%)	-0.215	0.273	0.245	0.503	0.505	0.219	0.472	0.415	0.022	0.360	-0.192	-0.037	0.303	-0.596	-0.569	-0.514	-0.098	-0.244	-0.668
mean discharge april relative to mean (%)	-0.044	0.007	0.016	0.466	-0.215	0.333	0.394	0.371	0.084	0.223	0.106	0.179	0.104	-0.286	-0.066	-0.170	0.336	0.001	-0.287
mean discharge may relative to mean (%)	0.229	-0.130	0.112	-0.202	-0.321	-0.108	-0.294	0.024	0.022	-0.244	0.024	0.166	-0.047	-0.290	0.482	0.343	0.495	-0.051	0.131
mean discharge june relative to mean (%)	0.154	-0.211	-0.190	-0.690	-0.073	-0.391	-0.537	-0.533	-0.111	-0.441	0.008	-0.155	-0.297	0.446	0.371	0.285	-0.059	0.048	0.686
mean discharge july relative to mean (%)	-0.225	0.241	0.264	0.495	0.585	0.178	0.348	0.340	0.013	0.405	-0.227	-0.030	0.297	-0.528	-0.847	-0.516	-0.144	-0.243	-0.678
mean discharge august relative to mean (%)	-0.120	-0.266	-0.144	-0.411	-0.355	-0.011	-0.266	-0.420	0.067	-0.330	0.269	0.168	-0.059	0.489	0.491	0.261	0.158	0.261	0.549
mean discharge september relative to mean (%)	0.067	-0.039	0.062	0.203	-0.327	0.062	0.050	-0.035	-0.093	0.132	-0.069	0.072	0.036	-0.125	0.226	0.047	0.101	-0.158	-0.106
mean discharge october relative to mean (%)	-0.129	0.163	0.140	0.452	0.474	0.214	0.422	0.426	0.012	0.458	-0.092	0.047	0.205	-0.474	-0.308	-0.362	0.017	-0.188	-0.529
log (x+1) mean discharge november relative to mean (%)	-0.174	0.132	0.145	0.582	0.146	0.349	0.522	0.463	0.076	0.430	-0.036	0.111	0.254	-0.501	-0.370	-0.382	0.083	-0.135	-0.610
log (x+1) mean discharge december relative to mean (%)	-0.216	0.215	0.215	0.588	0.452	0.327	0.492	0.441	0.092	0.388	-0.110	0.031	0.354	-0.474	-0.523	-0.421	-0.080	-0.146	-0.712
log (x+1) mean discharge january 1 yrs relative to average	-0.187	0.245	0.189	0.511	0.503	0.167	0.312	0.353	0.006	0.454	-0.220	-0.009	0.310	-0.473	-0.510	-0.474	-0.169	-0.198	-0.720
log (x+1) mean discharge february 1 yrs relative to average	-0.129	0.221	0.087	0.506	0.350	0.201	0.164	0.157	0.096	-0.048	0.084	0.393	-0.221	-0.358	-0.230	-0.103	0.059	0.259	-0.541
log (x+1) mean discharge march 1 yrs relative to average	-0.183	0.201	0.027	0.485	0.376	0.206	0.183	0.097	0.101	0.039	-0.097	0.079	0.315	-0.381	-0.281	-0.242	0.103	0.076	-0.535
log (x+1) mean discharge april 1 yrs relative to average	-0.327	0.145	-0.005	0.495	-0.413	0.220	0.497	0.303	0.051	0.306	-0.047	0.197	0.129	-0.476	-0.385	-0.422	0.152	-0.228	-0.482
mean discharge may 1 yrs relative to average	0.223	-0.138	0.068	-0.180	-0.410	-0.017	-0.234	0.059	0.095	-0.255	0.245	-0.045	-0.177	0.484	0.388	0.527	0.003	0.189	-0.420
mean discharge june 1 yrs relative to average	0.228	-0.199	-0.211	-0.549	-0.405	-0.185	-0.454	-0.463	0.008	-0.491	0.180	-0.044	-0.179	0.570	0.545	0.481	0.046	0.217	0.677
mean discharge july 1 yrs relative to average	0.001	0.012	-0.235	-0.340	0.014	-0.289	-0.378	-0.560	-0.214	-0.248	-0.167	-0.001	-0.124	0.146	0.128	0.106	-0.058	0.025	0.288
mean discharge august 1 yrs relative to average	-0.061	-0.122	-0.178	-0.539	0.079	-0.283	-0.416	-0.467	-0.105	-0.187	-0.008	-0.003	-0.157	0.270	0.144	0.241	-0.118	0.062	0.418
mean discharge september 1 yrs relative to average	-0.093	-0.007	0.065	-0.210	0.190	-0.274	-0.018	-0.059	-0.292	0.318	-0.334	-0.146	-0.166	-0.323	-0.087	-0.270	-0.103	-0.440	-0.101
mean discharge october 1 yrs relative to average	-0.054	0.056	0.100	0.639	-0.171	0.431	0.414	0.363	0.172	0.260	0.094	0.177	0.312	-0.311	-0.154	-0.210	0.306	0.800	-0.472
log (x+1) mean discharge november 1 yrs relative to average	-0.113	0.099	0.089	0.611	-0.300	0.353	0.512	0.423	0.080	0.421	0.000	0.159	0.246	-0.452	-0.252	-0.333	0.180	-0.073	-0.563
log (x+1) mean discharge december 1 yrs relative to average	-0.180	0.188	0.079	0.499	0.902	0.372	0.413	0.365	0.219	0.126	0.307	0.086	0.384	-0.150	-0.357	-0.136	-0.140	0.127	-0.543
max relative to mean (%)	-0.020	-0.242	-0.130	-0.222	-0.299	-0.144	-0.132	-0.005	0.077	-0.118	0.195	-0.089	-0.283	0.276	0.214	0.260	0.079	0.076	0.297
0.1x relative to mean (%)	0.141	-0.150	-0.249	-0.628	-0.139	-0.329	-0.436	-0.603	-0.116	-0.369	0.031	-0.064	-0.196	0.369	0.269	0.285	-0.035	0.046	0.649
95 perc. relative to mean (%)	0.123	-0.179	-0.141	-0.304	-0.134	-0.401	-0.128	-0.006	-0.360	-0.003	-0.195	-0.295	-0.449	0.043	0.171	0.209	0.085	0.203	0.284
log (x+1) 5 perc. relative to mean (%)	0.146	0.024	0.129	0.487	-0.124	0.542	0.074	0.099	0.403	-0.052	0.286	0.239	0.478	0.087	0.078	0.057	0.179	0.110	-0.242
difference min-max relative to mean (%)	-0.021	-0.241	-0.130	-0.223	-0.296	-0.147	-0.131	-0.006	0.074	-0.117	0.191	-0.091	-0.286	0.274	0.212	0.258	0.077	0.073	0.297
difference 95-5 percentile relative to mean (%)	0.086	-0.154	-0.141	-0.345	-0.109	-0.438	-0.119	-0.008	-0.379	0.006	-0.215	-0.301	-0.474	-0.043	0.143	0.027	0.051	0.194	0.277
difference 99-1 percentile relative to mean (%)	0.176	-0.197	-0.017	-0.133	-0.393	-0.226	-0.163	0.034	-0.185	-0.078	0.006	-0.173	-0.382	0.150	0.328	0.293			

959 **Table A.5.** Reduction of the 78 hydrological variables into principal components. Variables
 960 that are strongly related to PC axis 1 and 2 (PC scores >0.6 or <-0.6) are marked.

Importance of components		
	PC1	PC2
Eigenvalue	24.45	19.15
Proportion Explained	0.31	0.24
Cumulative Proportion	0.31	0.55
Importance of components		
	PC3	PC4
Eigenvalue	7.27	5.15
Proportion Explained	0.09	0.07
Cumulative Proportion	0.64	0.71
PC scores		
	PC1	PC2
<i>mean discharge</i>		
<i>average 5 years</i>		
january	0.746	0.174
february	0.733	0.008
march	0.685	0.326
april	0.167	0.599
may	-0.552	-0.153
june	-0.530	-0.528
july	-0.518	-0.511
august	-0.505	-0.388
september	-0.004	0.211
october	0.392	0.594
november	0.499	0.601
december	0.735	0.307
<i>one year before sampling</i>		
january	0.752	0.179
february	0.733	-0.250
march	0.666	-0.261
april	0.365	0.587
may	-0.556	-0.124
june	-0.556	-0.543
july	-0.165	-0.515
august	-0.401	-0.408
september	-0.028	0.351
october	0.449	0.398
november	0.429	0.609
december	0.688	-0.009
<i>magnitude of extremes</i>		
max	-0.581	0.304
min	0.412	-0.393
95 percentile	-0.589	0.366
5 percentile	0.518	-0.358
difference min-max	-0.583	0.306
difference 95-5 percentile	-0.602	0.374
difference 99-1 percentile	-0.627	0.345
75 percentile	0.034	-0.284
25 percentile	0.595	-0.232
average yearly max	-0.558	0.468
coefficient of variation yearly max	-0.456	-0.052
average yearly min	0.456	-0.367
coefficient of variation yearly min	-0.065	0.311
7 day max	-0.652	-0.046
7 day min	0.505	-0.408
<i>monthly maximum one year before sampling</i>		
january	0.404	0.589
february	0.698	-0.090
march	0.664	-0.241
april	0.178	0.693
may	-0.531	0.015
june	-0.509	-0.261
july	-0.252	-0.240
august	-0.412	0.279
september	-0.030	0.638
october	0.091	0.632
november	0.240	0.725
december	0.297	0.564
<i>monthly minimum one year before sampling</i>		
january	0.692	-0.272
february	0.684	-0.276
march	0.653	-0.237
april	0.581	-0.242
may	0.264	0.262
june	-0.444	-0.565
july	-0.135	-0.487
august	-0.109	-0.508
september	-0.031	-0.308
october	0.515	-0.140
november	0.495	0.006
december	0.647	-0.276
<i>timing of extremes</i>		
Julian day of max 1 year before sampling	0.316	0.351
days between sampling and last maximum	0.233	0.448
Julian day of min 1 year before sampling	0.238	-0.091
average Julian day maximum	0.011	-0.138
average Julian day minimum	0.291	-0.165
month with highest discharge	-0.203	0.237
<i>frequency and duration of high pulses (high pulse is > 0.9 percentile)</i>		
number of days with high pulses 1 year before sampling	-0.099	0.267
number of high pulses 1 year before sampling	0.133	0.591
total number of high pulses in 5 years	-0.047	0.567
average duration of high pulses (days)	0.036	-0.418
<i>rate of change</i>		
maximum rising limb	-0.550	0.433
minimum falling limb	0.542	-0.439
average rising limb	-0.270	0.727
average falling limb	0.202	-0.698
<i>base flow index</i>		
BFI 5 years	0.261	-0.719
BFI 1 year before sampling	0.272	-0.723

962 **Table A.6.** hydrological characteristics at 20 regulated and 20 unregulated sites. Site codes
963 refer to Table A.1.

		regulated sites																			
		109.2	12.137	12.2	12.8	16.1	16.155	16.51	19.72	2.129	2.484	2.611	21.21	25.6	27.13	30.8	38.2	36.31	50.11	6.9	8.2
95 perc. relative to mean (%)		355.5	228.8	330.5	294.5	242.8	360.9	195.0	151.2	274.5	283.1	154.4	242.5	319.3	174.6	345.2	400.6	295.2	272.6	343.3	383.8
5 perc. relative to mean (%)		9.9	40.2	13.1	6.2	21.1	13.6	21.6	12.1	12.1	12.1	12.1	12.1	12.1	12.1	12.1	12.1	12.1	12.1	12.1	12.1
max relative to mean (%)		2245.3	915.3	2076.0	1935.6	797.2	1334.7	164.6	316.3	2785.3	674.0	296.4	1570.7	379.4	254.4	3076.5	2197.8	1806.7	532.3	932.3	1565.2
min relative to mean (%)		7.1	5.7	10.3	0.0	10.9	2.3	19.7	5.0	5.2	5.9	18.0	2.6	0.1	20.0	0.0	0.2	0.4	3.8	12.4	6.0
difference min-max relative to mean (%)		2238.2	909.6	2065.7	1935.6	786.9	1332.4	175.4	310.6	2773.2	668.1	277.7	1557.1	379.3	234.4	3076.3	2197.6	1806.3	528.8	920.3	1559.2
difference 95-5 percentile relative to mean (%)		345.6	188.6	317.2	288.3	221.1	350.9	160.6	179.6	263.8	270.3	147.7	205.4	314.7	140.3	341.1	394.7	290.1	213.1	315.1	370.9
difference 99-1 percentile relative to mean (%)		577.3	419.9	735.9	531.3	392.3	702.7	333.7	205.0	600.0	408.4	146.4	451.7	342.8	165.7	793.9	792.6	484.4	300.2	716.3	675.3
75 perc. relative to mean (%)		126.1	100.0	113.0	131.7	111.4	122.7	112.1	107.8	136.3	158.8	118.0	107.5	160.4	145.2	119.9	117.6	129.8	189.7	112.4	105.6
25 perc. relative to mean (%)		20.9	67.6	22.7	17.7	59.3	26.8	66.8	21.8	37.1	31.1	79.3	50.2	16.4	58.3	21.9	15.6	26.9	22.4	36.7	25.1
average yearly max relative to mean discharge (%)		1131.7	604.9	1126.6	913.1	637.5	994.9	446.2	275.5	1247.1	495.4	232.4	799.0	361.6	204.4	2035.0	1520.8	697.2	422.3	620.5	1161.1
average yearly min relative to mean discharge (%)		13.5	15.8	11.9	5.8	12.9	9.3	24.6	8.2	13.5	10.6	39.9	26.3	1.9	29.4	3.8	3.7	5.1	8.3	22.0	12.4
mean discharge january relative to mean (%)		20.5	73.4	20.2	13.5	84.2	22.7	82.0	166.1	19.9	41.5	84.9	47.3	107.8	138.1	49.7	81.6	54.7	37.3	35.1	31.0
mean discharge february relative to mean (%)		21.5	70.4	15.7	11.1	84.6	20.5	87.0	154.5	16.7	39.5	83.0	45.8	124.6	112.9	43.3	44.9	31.8	29.5	34.2	17.2
mean discharge march relative to mean (%)		27.4	64.5	23.1	26.6	78.5	39.7	85.5	141.2	18.6	33.6	76.4	55.8	90.9	110.1	65.6	87.9	68.1	37.2	36.9	50.0
mean discharge april relative to mean (%)		62.4	58.7	111.7	125.6	122.8	144.0	102.9	83.6	107.8	32.3	78.0	109.2	51.4	88.4	145.0	128.2	122.6	61.3	161.3	252.1
mean discharge may relative to mean (%)		219.9	178.0	300.5	260.1	129.8	274.4	127.3	62.1	237.0	138.2	128.5	224.7	86.8	74.1	188.6	104.8	159.1	157.8	93.2	111.0
mean discharge june relative to mean (%)		314.0	171.3	144.0	123.2	75.1	138.4	73.2	45.0	212.4	239.7	138.9	140.2	196.2	0.0	79.8	44.5	95.3	208.1	68.9	73.4
mean discharge july relative to mean (%)		214.8	111.8	119.8	118.3	114.8	104.0	97.8	38.1	158.8	229.7	116.7	120.5	165.0	49.1	77.0	64.3	97.1	200.9	81.4	84.4
mean discharge august relative to mean (%)		131.5	114.1	164.7	153.2	111.3	137.4	124.3	49.9	163.0	173.3	118.0	105.9	140.5	58.4	100.8	77.1	107.9	195.0	99.6	135.6
mean discharge september relative to mean (%)		82.9	102.6	133.9	123.3	105.2	117.0	116.4	69.3	108.2	115.7	110.6	108.8	93.9	109.9	111.1	154.8	140.4	130.0	23.4	116.7
mean discharge october relative to mean (%)		52.7	94.6	75.1	85.3	101.2	101.0	106.6	118.6	78.8	67.3	102.9	104.0	33.3	124.7	128.5	160.3	120.2	62.4	147.8	117.8
mean discharge november relative to mean (%)		32.0	79.7	55.3	92.6	108.3	70.6	105.5	129.3	47.5	42.8	88.8	84.1	41.2	137.3	140.3	164.9	138.0	37.6	145.3	154.8
mean discharge december relative to mean (%)		20.6	78.8	30.4	60.1	83.6	31.1	90.7	150.9	26.5	42.3	72.4	50.7	78.3	128.1	67.2	85.1	61.9	36.0	46.7	56.5
max discharge january 1 yrs relative to annual mean		0.17	0.79	0.31	0.24	1.09	0.39	0.96	1.91	0.11	0.55	0.94	0.63	1.54	1.61	2.63	5.10	4.72	0.45	0.71	0.64
max discharge february 1 yrs relative to annual mean		0.11	0.76	0.19	0.12	0.95	0.26	0.99	1.90	0.07	0.42	0.84	0.52	2.06	1.46	0.00	0.40	1.53	0.28	0.36	0.21
max discharge march 1 yrs relative to annual mean		0.73	0.14	0.11	0.07	0.16	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11
max discharge april 1 yrs relative to annual mean		0.94	0.62	0.85	2.39	1.91	1.71	1.14	1.74	3.08	2.02	1.14	1.53	2.02	1.12	8.28	6.73	5.08	2.37	3.27	0.64
max discharge may 1 yrs relative to annual mean		4.92	7.91	20.76	19.36	7.97	13.35	5.50	2.64	20.81	4.66	2.38	15.71	0.79	1.39	16.69	4.25	7.51	5.73	1.81	15.65
max discharge june 1 yrs relative to annual mean		6.50	5.40	5.40	4.45	4.45	4.45	4.45	4.45	4.45	4.45	4.45	4.45	4.45	4.45	4.45	4.45	4.45	4.45	4.45	4.45
max discharge july 1 yrs relative to annual mean		1.89	1.43	3.07	2.03	1.54	2.64	1.61	1.54	1.94	2.23	1.30	1.17	3.43	0.37	0.62	1.18	1.35	1.91	6.05	1.96
max discharge august 1 yrs relative to annual mean		2.95	1.70	3.95	2.03	2.36	3.20	1.65	1.29	5.17	2.78	1.26	4.27	3.09	1.09	5.25	3.30	5.01	2.28	4.99	2.54
max discharge september 1 yrs relative to annual mean		0.95	1.10	1.40	1.35	2.14	1.25	1.12	1.99	1.24	2.36	1.34	1.97	0.75	1.77	7.73	9.03	3.79	2.98	2.05	3.14
max discharge october 1 yrs relative to annual mean		0.45	1.03	1.60	2.34	2.50	3.54	1.86	2.49	0.70	4.47	1.55	2.52	0.96	1.99	7.17	6.47	3.77	1.22	4.64	12.99
max discharge november 1 yrs relative to annual mean		0.24	0.83	0.66	5.29	1.05	0.55	1.24	1.91	0.34	0.49	1.01	0.62	1.42	1.55	2.25	7.52	4.79	0.39	0.33	0.62
max discharge december 1 yrs relative to annual mean		0.09	0.70	0.18	0.07	0.52	0.18	0.50	1.51	0.07	0.37	0.83	0.48	0.09	0.88	0.00	0.06	0.02	0.25	0.25	0.19
min discharge january 1 yrs relative to average		0.09	0.73	0.14	0.10	0.55	0.10	0.62	1.64	0.06	0.37	0.78	0.48	0.05	0.88	0.00	0.08	0.06	0.24	0.28	0.14
min discharge february 1 yrs relative to average		0.11	0.07	0.10	0.07	0.16	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11
min discharge march 1 yrs relative to average		0.07	0.06	0.10	0.07	0.13	0.11	0.42	0.31	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13
min discharge april 1 yrs relative to average		0.14	0.15	0.70	0.69	0.60	1.02	0.85	0.12	0.50	1.13	1.16	0.46	0.11	0.35	0.28	0.22	0.81	0.11	0.54	0.69
min discharge may 1 yrs relative to average		1.48	0.90	0.73	0.76	0.55	0.89	0.42	0.09	1.44	1.40	1.14	0.89	0.09	0.32	0.44	0.12	0.76	1.77	0.42	0.30
min discharge june 1 yrs relative to average		0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38
min discharge july 1 yrs relative to average		0.46	0.43	0.30	0.14	0.22	0.04	0.55	0.11	1.00	0.96	0.76	0.81	0.05	0.32	0.25	0.09	0.72	1.68	0.36	0.13
min discharge august 1 yrs relative to average		0.42	0.53	0.47	0.48	0.13	0.30	0.20	0.12	0.72	0.25	0.92	0.82	0.05	0.68	0.16	0.20	0.75	0.27	0.42	0.25
min discharge september 1 yrs relative to average		0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24	0.24
min discharge october 1 yrs relative to average		0.15	0.47	0.51	0.65	0.71	0.62	0.87	0.49	0.34	0.13	0.82	0.51	1.00	0.27	0.10	0.21	0.25	0.13	0.41	0.65
min discharge november 1 yrs relative to average		0.24	0.74	0.30	0.18	0.55	0.30	0.59	1.18	0.22	0.37	0.70	0.44	0.03	0.86	0.07	0.08	0.12	0.18	0.27	0.25
min discharge december 1 yrs relative to average		0.13	0.74	0.23	0.15	0.87	0.26	0.83	1.74	0.09	0.43	0.88	0.54	0.95	1.29	0.38	0.86	0.71	0.31	0.34	0.29
mean discharge january 1 yrs relative to average		0.09	0.74	0.16	0.12	0.81	0.13	0.93	1.78	0.07	0.39	0.81	0.50	1.20	1.04	0.00	0.13	0.17	0.26	0.33	0.16
mean discharge february 1 yrs relative to average		0.09	0.70	0.12	0.09	0.70	0.10	0.69	1.77	0.06	0.33	0.74	0.47	1.72	0.80	0.00	0.09	0.07	0.21	0.33	0.13
mean discharge march 1 yrs relative to average		0.39	0.30	0.37	0.35	0.37	0.35	0.37	0.35	0.37	0.35	0.37	0.35	0.37	0.35	0.37	0.35	0.37	0.35	0.37	0.35
mean discharge april 1 yrs relative to average		1.49	3.20	5.51	4.38	2.51	4.81	2.45	0.79	4.21	2.11	1.47	4.31	0.43	1.71	3.25	1.43	2.35	1.86	3.17	2.53
mean discharge may 1 yrs relative to average		2.58	2.06	2.30	1.77	1.43	2.52	1.04	0.94	2.62	2.36	1.44	1.55	1.01	0.54	1.74	0.29	0.94	1.59	1.59	1.32
mean discharge june 1 yrs relative to average		0.82	0.51	0.34	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32
mean discharge july 1 yrs relative to average		1.09	1.02	1.30	0.98	0.80	0.64	1.07	3.32	1.67	1.85	0.98	1.24	1.71	0.36	0.98	0.64	1.28	1.80	0.43	0.58
mean discharge august 1 yrs relative to average		0.69	0.73	0.68	0.79	0.54	0.54	0.44	0.28	0.93	1.21	1.05	1.02	0.24	1.26	1.43	2.26	1.40	1.33	1.35	0.57
mean discharge september 1 yrs relative to average		1.0	0.78	0.81	0.81	1.16	1.16	1.16	1.16	1.16	1.16	1.16	1.16	1.16	1.16	1.16	1.16	1.16	1.16	1.16	1.16
mean discharge october 1 yrs relative to average		1.30	0.84	0.88	1.17	1.37	1.49	1.37	1.70	0.57	0.25	1.11	0.90	0.57	1.13	1.69	1.74	0.42	3.15	2.81	2.81
mean discharge november 1 yrs relative to average		0.19	0.80	0.41	1.27	0.86	0.35	0.94	1.69	0.26											

