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Juncus bulbosus **nuisance growth in oligotrophic freshwater ecosystems: different triggers for the same phenomenon in rivers and lakes?**

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Abstract

Since the 1980s nuisance growth of the aquatic macrophyte *Juncus bulbosus* has been observed in an increasing number of rivers and lakes in Europe. Freshwater acidification, lake liming, as well as the impact of hydropower plants and climate-related parameters have previously been assumed to have caused *J. bulbosus* mass development, but are unlikely to be the sole reason for today's phenomenon. To explore causalities for *J. bulbosus* mass development and to assess whether or not different patterns emerge in rivers and lakes, we analyzed macrophyte vegetation, periphyton coverage, water and sediment chemistry, catchment characteristics, and *J. bulbosus* elemental composition in 17 lakes and 28 river sites in southern Norway. We found that *J. bulbosus* mass development generally is a phenomenon of the most phosphorus- and calcium-poor rivers and lakes. This likely is a result of increased competition from other macrophyte species in all but the very most oligotrophic and acidic ecosystems. Despite a large number of measured parameters, however, we still lack clear correlates to *J. bulbosus* success. Nevertheless, our results with respect to changes in water CO_2 and plant carbon content were consistent with literature suggesting CO_2 as the most likely factor causing *J. bulbosus* mass development in lakes. While *J. bulbosus* seems to be carbon-limited in lakes with low *J. bulbosus* abundance, we have no such indications in high-abundance lakes. For rivers, our study indicates that the factor most closely connected to *J. bulbosus* success is a slightly enhanced NH_4^+ supply. We suggest that different factors may be responsible for *J. bulbosus* nuisance growth in rivers and lakes.

1. Introduction

Juncus bulbosus L. is a perennial macrophyte native to Europe and North Africa and can inhabit both aquatic and terrestrial habitats (Casper and Krausch, 1980). The species is described as preferring nutrient and calcium poor, acidic water (Casper and Krausch, 1980; Johansen et al., 2000). Its ecological amplitude, however, extends to calcareous, eutrophic and even brackish waters (Olsen, 1950 and literature cited therein).

Since the 1980s nuisance growth of *J. bulbosus* has been observed in a number of rivers and lakes in Europe (Roelofs et al., 1994; Johansen et al., 2000; Brandrud, 2002). In lakes, the enhanced growth of *J. bulbosus* often occurred together with *Sphagnum* sp. and at the expense of other macrophyte species, and has been related to acid deposition with sulfate and ammonium as major components (Melzer, 1984; Schuurkes et al., 1987). The resulting initial increase in NH_4^+ and CO_2 concentrations have been suggested to favor *J. bulbosus* compared to other macrophyte species (Roelofs, 1983; Roelofs et al., 1995). In addition, experimental studies and field observations have shown that lake liming combined with re-acidification of the water can promote *J. bulbosus* growth, since liming leads to temporary increased levels of CO_2 and NH_4^+ (Roelofs et al., 1995; Lucassen et al., 1999). Roelofs et al. (1984) concluded that, though NH_4^+ enrichment indeed seemed to favor plant growth, water CO_2 concentration was the primary trigger for *J. bulbosus* nuisance growth in lakes, since phosphate and/or NH_4^+ enrichment without concomitant CO_2 enrichment did not lead to an increase in *J. bulbosus* biomass.

Fewer data are available from rivers than from lakes. Increased *J. bulbosus* growth in South Norwegian rivers is reported to have begun around the 1960s to 1980s (Johansen et al., 2000), and several hypotheses have been advocated to explain these changes: mild winters leading to less ice erosion and thus to a higher persistence of *J. bulbosus* biomass (Johansen et al., 2000; Hindar et al., 2003), hydropower plants with resulting alterations in flow patterns, flow velocity and ice cover (Johansen et al., 2000; Hindar et al., 2003), as well as increased NH_4^+ concentrations (Hindar et al., 2003). In contrast to lakes, liming has not been considered a likely cause for nuisance growth in rivers (Johansen et al., 2000).

Lakes in Norway exhibit clear signs of recovery from acidification since the 1990s (Skjelkvåle et al., 1998; 2007), and currently massive growth of *J. bulbosus* also occurs in non-limed Norwegian lakes. Thus, acidification and liming, which previously have been assumed to cause *J. bulbosus* nuisance growth in lakes (Schuurkes et al., 1987; Roelofs et al.,

1995; Lucassen et al., 1999), probably are not the sole reason for the mass occurrence. We analyzed macrophyte vegetation, periphyton coverage, water and sediment chemistry, catchment characteristics and *J. bulbosus* elemental composition in 17 lakes and 28 river sites in Southern Norway. Sampling was conducted in both 2008 and 2010 at the same sampling sites. The main objectives of this study were i) to explore causality for increased *J. bulbosus* growth, and ii) to assess whether different patterns emerge in rivers and lakes. We hypothesized that different primary triggers might be responsible for *J. bulbosus* mass development in rivers and lakes.

2. Materials and Methods

2.1 Description of *Juncus bulbosus*

J. bulbosus exhibits an extreme variation in morphology (Glück, 1936; Roćków, 2008). The terrestrial form (f. *terrestris*) grows as short green or reddish meadows, plants of the submerged form (f. *submersus*) grow up to 2 m long and can have up to 60 cm long leaves, and the floating form (f. *fluitans*) develops floating mats with richly branched stems and plant tips growing above the water surface (Casper and Krausch, 1980). Aquatic plants of *J. bulbosus* initially grow as a small rosette 10-20 cm in length. Stems can, however, emerge from the rootstalk, and the plant often develops new rosettes and roots on each node of the stem (Casper and Krausch, 1980; Johansen et al., 2000).

2.2 Field work

This study is based on a survey of 17 lakes and 28 sites from 15 different rivers in South Norway (Fig. 1). Each river site was visited twice, in July 2008 and August 2010 and all but one lake site were visited three times, in June 2008, September 2008 and July 2010. The remaining lake site was visited in June 2008 only. At each river site, macrophyte vegetation was registered along a stretch of approximately 50 m, while at lake sites, a transect of approximately 20 m breadth was investigated to the depth where we could no longer see the bottom. Due to the generally high water transparency in most Norwegian lakes this depth usually corresponds to or is greater than the lower vegetation limit. Each lake site was situated at the site of most abundant *J. bulbosus* growth in the respective lake, based on information from previous investigations. At each lake and river site the abundance of *J. bulbosus* growth forms (rosette plants/short stems (< 40 cm)/long stems (> 40 cm)/fresh surface mats/old surface mats) was registered according to a 3-point scale: 1 = sparsely; 2 = covering large

parts; 3 = dominating the site. For data analyses, fresh and old mats were later combined. At lake sites, the abundance of other macrophyte species was recorded according to a 5-point scale (1 = very rare, 2 = infrequent, 3 = common, 4 = frequent, 5 = abundant, predominant), and the sum of isoetids was calculated as the total sum of abundance of *Isoetes*, *Lobelia* and *Littorella* species. We also noted presence or absence of small but clearly visible periphytic algae on *J. bulbosus* leaves and of large amounts of filamentous algae around *J. bulbosus* plants. At river sites, flow velocity was estimated as 1=low, 2=medium, 3=high, and at lake sites Secchi depth was recorded. At each site, a sediment core of 5.5 cm in diameter and approximately 10 cm length was taken at the site of most prolific *J. bulbosus* growth. Due to coarse sediment, we were unable to sample sediment at 6 river sites (5 with low abundance and 1 site with high abundance of *J. bulbosus*). The sediment samples were frozen in dry ice immediately after sampling and kept frozen until analysis. Water samples were collected at approximately 10 cm depth at each site, and $HgCl_2$ was used to preserve samples for CO_2 analysis in 125 ml serum vials with gas-tight stoppers. In addition, a random *J. bulbosus* plant was collected at each site from the most abundant stand, dried and later analysed for carbon (C), nitrogen (N) and phosphorus (P). Sediment, water chemistry and plant samples in 2008 and 2010 were sampled within few meters distance, i.e. within the same site of most prolific growth.

2.3 Water and sediment analyses

Water chemical parameters were analysed at the Norwegian Institute for Water Research (NIVA) according to standard methods (pH: NS 4720; conductivity: NS-ISO 7888; Calcium (Ca), nitrate (NO_3^-), and ammonium (NH_4^+): ion chromatography according to NS-EN ISO 10304-1 and NS-EN-ISO 14911; total organic carbon (TOC): NS-ISO 8245; dissolved inorganic carbon (DIC): NS-EN 1484; CO_2: Standard Methods 4500-CO2, 4-12-4-18; Total nitrogen (TotN): NS 4743; Total phosphorus (TotP): NS 4725; phosphate (PO_4^{3-}): NS 4724). Dissolved inorganic nitrogen (DIN) was calculated as the sum of NO_3^- and NH_4^+.

Sediment porewater was extracted from the thawed sediments through centrifugation and analysed for PO_4^{3-}, NO_3^-, and NH_4^+. Porewater NH_4^+ was analysed using protocol B from Holmes et al. (1999). Porewater NO_3^- and PO_4^{3-} were analysed using an auto-analyser with applications G-297-03 for PO_4^{3-} and G-172-96 for NO_3^- (Auto-analyser 3, SEAL Analytical/BRAN LUEBBE, Norderstedt, Germany). To account for sediment water content,

we calculated sediment nutrient concentrations as pore-water nutrients per volume sediment. Sediment water content was calculated as (wet weight minus dry weight)/wet weight. Dry weight was measured after drying the sediments at 105°C for 24 hours. Organic content was measured as (dry weight minus ash free dry weight)/dry weight. Ash free dry weight was measured after burning the dried sediment sample in a muffle furnace for 2h at 450°C and cooling the sample to room temperature in a desiccator.

2.4 Plant elemental composition

For the 2008 samples, the entire plant was analysed for carbon (C), nitrogen (N), and phosphorus (P), whereas the plants sampled in 2010 were analysed separately for both roots and shoots (the transition zone between the root and the shoot was not analysed). Fresh, vital plants were collected, manually cleaned of detritus and periphyton in the field, dried and stored until elemental analyses. The dried plants were ground 45 sec at 6500 rpm on a Precellys 24 (Bertin Technologies, Montigny, France), and C and N were analysed on an element analyser (Flash EA 1112 NC Analyser, ThermoFisher Scientific, MA, US). P was analysed in an autoanalyzer with application G-297-03 (Autoanalyzer 3, SEAL Analytical/BRAN LUEBBE, Norderstedt, Germany). All results are reported as % of dry weight.

2.5 Catchment data

Catchment boundaries for each investigated lake and river site were delineated according to the procedures described in Larsen et al. (2011a), and data on annual average temperature, precipitation, runoff and satellite derived normalized difference vegetation index (NDVI) as well as data on terrain slope, area and altitude was obtained according to Larsen et al. (2011b). The NDVI reflects the density of plant growth, with low values corresponding to barren rock or snow, and high values typically indicating forests. Atmospheric nitrogen deposition was averaged for each catchment from a digital map of yearly, accumulated total atmospheric nitrogen deposition (including dry deposition) for 1995. The nitrogen deposition map was constructed by spatial interpolation (kriging with a spherical semivariogram model) on 1° x 1° gridded output data from the Unified EMEP MSC-W modelling system (http://www.emep.int/). Data on solar, UVA and UVB irradiation (based on yearly averages of global horizontal irradiation for the period 1981-1990) were obtained from the Photovoltaic

Geographic Information System (PVGIS) of the European Commission Joint Research Centre (JRC) (http://re.jrc.ec.europa.eu/pvgis/) (Súri et al., 2005). County governors assisted with information on river and lake liming. Information on hydropower development was obtained from the Norwegian Water Resources and Energy Directorate (NVE), in collaboration with local hydropower companies and county governors.

2.6 Data handling

A site was defined as having a high abundance of *J. bulbosus* when either large stems or surface mats dominated the site (i.e. abundance was noted as 3), or large stems and mats together dominated the site (i.e. the sum of abundances of large stems, old mats and fresh mats was 5 or more). This definition matches the visual impression in the field, that a site is "overgrown" with *J. bulbosus*. When a site was categorized as "high abundance" during one sampling event but not the other, the site was generally categorized as "high abundance". Using these categories, we had a dataset of 21 river sites and 5 lakes where *J. bulbosus* was present in low abundance, and 7 river sites and 12 lakes where it was present in high abundance (Fig. 1).

To explore the structure in our data, we computed a PCA on the pooled data from rivers and lakes, using average values per site for water and sediment chemistry, plant elemental composition, and catchment data. Due to some missing values, only 15 lakes (four "low abundance", 11 "high abundance"), and 21 river sites (15 "low abundance", six "high abundance") were included in the PCA. After exploratory analysis, data were log- or square-root-transformed where necessary to improve normality and homoscedasticity (Table 1). The PCA was computed using R version 2.14.2 (R Development Core Team, 2012), extended with the "vegan" package 2.0-4 (Oksanen et al., 2012). We also tested models based on *J. bulbosus* growth forms and their abundances, but they all had very low explanatory power (unpublished data).

To test whether different patterns emerge in rivers and lakes, the dataset was then divided. To explore causality for increased *J. bulbosus* growth, we also calculated the differences in chemical parameters between the two (rivers) and three (lakes) sampling events. Due to some missing values, parameters had to be analyzed one by one instead of using a multivariate approach. Because most of the measured variables in the divided datasets were not normally distributed and normal distribution for some of these parameters was not achieved by

transformation either, non-parametric Mann-Whitney U tests were used when testing for differences between high-abundance and low-abundance sites, and between river and lake locations. Fisher's test was used for binomial variables. Except for the differences between sampling events, average values per site were used for the two (rivers) or three (lakes) sampling events. These tests were performed using STATISTICA 10. Because each analysis represented a separate hypothesis, there was no need to adjust α for multiple testing (Perneger, 1998).

3. Results

3.1 Characterization of high-abundance versus low-abundance sites

The main growth forms at lake and river sites with low abundance of *J. bulbosus* were rosette plants and small stems, while lake and river sites with high abundance were dominated by small and large stems. Not surprisingly, high-abundance lake and river sites were generally characterized by a higher abundance of surface mats and large and small stems than low-abundance lake and river sites. In contrast, we observed no such difference in the abundance of rosette plants between high-abundance and low-abundance lakes and rivers (data not shown). The abundance of mats and large stems increased slightly from 2008 to 2010 at high-abundance lake and river sites, whereas the abundance of small stems and rosette plants decreased slightly. No clear patterns were observed in low-abundance lakes and rivers (data not shown).

A PCA of the water and sediment chemistry, plant elemental composition, and catchment data separated river and lake sites along PC1 (Fig. 2a), while sites with high abundance of *J. bulbosus* tended to have low values along both PC3 and PC4 (Fig. 2b). Separation of river and lake sites was largely due to catchment parameters, but river sites also tended to have lower water C, N and P concentrations, as well as a less organic sediment and higher shoot N content than lake sites (Table 1, PC1). Sites with high abundance of *J. bulbosus* tended to have lower water P concentrations, lower precipitation, and a lower plant N and P content (Table 1, PC3). Thus, sites with high abundance of *J. bulbosus* can generally be characterized as being among the most oligotrophic, phosphorus-poor in our dataset. In addition, sites with high abundance of *J. bulbosus* were characterized as being acidic and Ca-poor (Table 1, PC4). So, overall, *J. bulbosus* mass development indeed appears to occur in what is usually regarded as the most oligotrophic rivers and lakes in Norway.

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Since the most obvious pattern emerging in the PCA was the separation among river and lake sites, we subsequently analyzed rivers and lakes separately. Due to missing values, however, parameters had to be analyzed one by one instead of using a multivariate approach. The general pattern from the PCA (low water P- and Ca-concentrations, low pH, as well as low plant N and P content at sites with high abundance of *J. bulbosus*) is reflected in Table 2, but the differences in these parameters among sites with high and low abundance were not significant. However, river sites with high abundance of *J. bulbosus* had a higher sediment NH_4^+ content but lower sediment NO_3^- concentration than river sites with low abundance of *J. bulbosus,* and they were less limed (Table 2). Also for lakes, the general pattern from the PCA is reflected in Table 3, but the differences were not significant. Lakes with high abundance of *J. bulbosus* were characterized by steep catchment morphology, however. In addition to the parameters given in Tables 2 and 3, we calculated plant CNP ratios. Again, we observed no significant differences between sites of high and low abundance (data not shown).

Reflecting the general pattern from the PCA, rivers generally had a lower conductivity and water TotN concentration, as well as a lower sediment water and organic content than lakes, and *J. bulbosus* shoots from rivers had a higher N-content (Table 4). This was true for both high- and low-abundance sites. River sites generally had a higher pH than lake sites, but this difference was only significant at sites with high abundance of *J. bulbosus*. An important additional result emerges for water NH_4^+ concentrations, however: low-abundance river sites had significantly lower water NH_4^+ concentrations than low-abundance lake sites, but there was no significant difference at high-abundance sites (Table 4, Fig. 3).

3.2 Differences in sediment and water chemistry between sampling events

We calculated the differences in all measured water and sediment chemical variables and the plant CNP composition between sampling events, and tested if the observed changes were different between high-abundance and low-abundance sites. In four instances, we observed significant differences between high-abundance and low-abundance sites. At river sites with high abundance of *J. bulbosus*, sediment NH_4^{+}-N increased from 2008 to 2010 by 0.502 ± 0.514 g m^{-3}, compared to a decrease of 0.109 ± 0.324 g m^{-3} at low-abundance sites (Fig. 4a; p=0.046 that high-abundance sites change differently between sampling events from low-abundance sites). Water pH also increased by 0.38 ± 0.12 at high-abundance sites, compared

to an increase of only 0.15 ± 0.19 at low-abundance sites (p=0.004 for the difference in change; data not shown).

In lakes with high abundance of *J. bulbosus*, water CO_2 concentrations did not change from spring 2008 to summer 2010 (we calculated an average decrease of 0.04 ± 0.11 mg L^{-1}), whereas it decreased by 0.31 ± 0.12 mg L^{-1} in low-abundance lakes during the same period (Fig. 4b; p=0.005 for the difference in change). The %C in *J. bulbosus* plants slightly increased from spring to autumn 2008 (0.73 ± 2.12 %C) in high-abundance lakes, but decreased by 1.83 ± 2.11 in low-abundance lakes (Fig. 4c; p=0.031).

4. Discussion

Our data suggest that *J. bulbosus* mass development occurs in the most phosphorus- and Ca-poor rivers and lakes. For lakes, this result is supported by a macrophyte index, which also suggested that the most problematic growth occurred in the most oligotrophic lakes (unpublished data). Although this is the ecological niche of *J. bulbosus*, increased plant growth in the most oligotrophic environments might seem counter-intuitive at first glance (note that eutrophication is defined as "the enrichment of water by nutrients … causing accelerated growth of … higher forms of plant life …" (European Commission, 2009) while we here show an accelerated growth of *J. bulbosus* in ecosystems where water nutrient concentrations are generally low). We suggest this could be a result of competition from other macrophyte species. In all but the very most acidic and phosphorus-poor environments, other macrophyte species capable of building tall stands, like e.g. *Potamogeton* sp. or *Myriophyllum* sp., compete with *J. bulbosus* for nutrients and light. Thus, they likely can prevent the development of massive *J. bulbosus* stands. In contrast, the most acidic and phosphorus-poor freshwater ecosystems in Norway are generally dominated by slow growing isoetids. In these ecosystems, *J. bulbosus* is the only species capable of building tall stands and thus of completely dominating the macrophyte vegetation. However, the fact that increased growth of *J. bulbosus* indeed occurs in the most acidic, nutrient poor environments makes detecting possible causes for this increased growth based on field measurements a tricky undertaking. Obviously, relatively more C, N, and P was incorporated in the *J. bulbosus* biomass of high-abundance lakes and rivers, because it clearly is more abundant while plant % C, N and P only slightly differ (Tables 2, 3). If an additional nutrient supply should be fully incorporated into plant biomass, however, this will not be reflected in increased water or sediment nutrient

concentrations. We suggest that the key to explaining *J. bulbosus* nuisance growth probably lies in measuring nutrient supply rather than concentrations. This could then demonstrate a limited nutrient supply in *Juncus*-dominated lakes, where all can be assimilated by this species, and a shift towards other plants at higher loading.

Juncus bulbosus **nuisance growth in rivers**

However, our results give some indications with respect to the most likely causes for increased *J. bulbosus* growth, and also that different primary triggers could be responsible in rivers compared to lakes. Rivers with high abundance of *J. bulbosus* were generally characterized by sediments having higher NH_4^+ and lower NO_3^- concentrations than low-abundance sites (Table 2). In addition, sediment NH_4^+ concentrations at high-abundance sites tended to increase from 2008 to 2010, compared to rather stable concentrations at low-abundance sites (Fig. 4a). Furthermore, there were significantly lower water NH_4^+ concentrations in low-abundance river sites compared to lakes, but no difference at high-abundance sites (Fig. 3). These results collectively point towards NH_4^+ as an important factor for enhanced *J. bulbosus* growth in rivers, while no other factors except liming are even close to being supported. NH_4^+ is usually rapidly removed in streams, often within a few tens to hundreds of meters (Peterson et al., 2001), such that lower NH_4^+ concentrations in rivers compared to lakes are not surprising. We therefore suggest that the relatively high NH_4^+ concentrations measured in rivers with high abundance of *J. bulbosus* are probably enhanced compared to background conditions. *J. bulbosus* has been shown to prefer NH_4^+ over NO_3^- as its N-source and it has also been shown that NH_4^+ can be taken up through both leaves and roots (Schuurkes et al., 1986), such that both an enrichment of water and sediment NH_4^+ can lead to increased plant growth. The importance of NH_4^+ for *J. bulbosus* nuisance growth was already assumed by Roelofs et al. (1995), Lucassen et al. (1999), and Brandrud (2002) and our own unpublished findings of a controlled growth experiment support the importance of NH_4^+ for *J. bulbosus* growth. In the present study, shoots of *J. bulbosus* river plants generally had a higher N-content than lake plants (Table 4). This also could indicate an importance of nitrogen-nutrition for *J. bulbosus* growth in rivers. The fact that we were unable to measure a significant difference in water NH_4^+ concentrations between nuisance and not-nuisance rivers, is likely explained by the typically rapid removal of NH_4^+ in streams, which often occurs within a few tens to hundreds of meters (Peterson et al., 2001). *J. bulbosus* very likely plays an important role in that removal.

River macrophytes are, however, well known to modify their own sediment by trapping particles from the water column (Kleeberg et al., 2010). Consequently, NH_4^+-rich material can be accumulated in dense *J. bulbosus* stands, such that enhanced sediment NH_4^+ concentrations would be an effect of, rather than a cause for, *J. bulbosus* nuisance growth. While this is true for sediments, it is unlikely that enhanced water NH_4^+ concentrations, as suggested by the results presented in Fig. 3, can actually be caused by dense *J. bulbosus* stands in rivers. Although there is a theoretical possibility of sediment porewater diffusing into the water column and thereby causing enhanced water NH_4^+ concentrations, the flow velocity and discharge of rivers in Norway, together with the known rapid removal of NH_4^+ in streams (Peterson et al., 2001), renders this possibility unlikely.

In summary, our results fit with published literature on *J. bulbosus* and cautiously support the following scenario; that an increase in biomass of *J. bulbosus* may be a result of an enhanced supply of NH_4^+. In contrast to earlier works, who directly assumed increased ammoniumsulfate deposition to be responsible for increased water NH_4^+- concentrations and *J. bulbosus* nuisance growth (Schuurkes et al., 1987), we did not find any direct influence from N-deposition (Table 2). This is probably due to the influence of climate and vegetation, as there is often no direct correlation between N-deposition and stream-N in Norway (de Wit et al., 2008). NH_4^+ input to rivers might instead be due to direct causes, e.g. treated wastewater in rural areas (scattered settlement in rural areas, with concomitant small-scale wastewater treatment is a common phenomenon in Norway, see e.g. Paruch et al., 2011), or runoff from cattle grazed areas (we in fact observed cattle grazing in the immediate surrounding of at least some of the river nuisance sites). Increased NH_4^+ supply might also be a result of reduced flow velocities in weir basins, leading to enhanced sedimentation of nutrient-rich material and a concomitant increase in supply of sediment NH_4^+. Irrespective of NH_4^+-origin will the initially enhanced *J. bulbosus* biomass likely start a positive feed-back mechanism: Dense stands will trap more fine sediment, thus leading to an even better supply of nutrients to the plants.

In contrast to lakes is direct liming from lime-dosers unlikely to trigger *J. bulbosus* nuisance growth in rivers. This was already suspected by Johansen et al. (2000) and Brandrud (2002). On the contrary, in our dataset, five of seven high-abundance sites were not limed, as opposed to only three of 21 low-abundance sites (see also Table 2, liming code). In lakes, liming leads to a higher availability of carbon dioxide in the sediment, partly owing to dissolution of carbonates, and partly by inducing anaerobic decomposition of organic matter and the

consequent reduction of iron (III) hydroxides in the iron-rich sediment which generates in-lake alkalinity (Lucassen et al., 2012). In contrast, the typically fast flow of Norwegian rivers should prevent major anaerobic decomposition in the sediment, as well as a significant sedimentation of carbonate rich material. Our dataset is too small to draw any conclusions on whether liming could actually prevent *J. bulbosus* nuisance growth in rivers, e.g. via increased competition by other macrophytes. However, such an effect, if occurring, would likely only prevent the massive growth of *J. bulbosus* at the expense of an increased growth of other macrophyte species. The different proportion of limed sites, with most high-abundance sites being not limed and most low-abundance sites being limed, likely explains the observed larger increase in pH from July 2008 to August 2010 at high-abundance sites compared to low-abundance sites. Calcium-poor rivers in southern Norway usually exhibit annual variations in pH with generally lowest values in spring and highest values in late summer/early autumn (DN, 2011). In contrast, pH in limed rivers varies less (DN, 2011), thus explaining the relatively small difference between July 2008 and August 2010.

Juncus bulbosus nuisance growth in lakes

There was no significant difference in the abundance of epiphytic algae on *J. bulbosus* between high- and low-abundance lake sites and plants with and without epiphytes were found in both high- and low-abundance lake sites (Table 3). Thus, in contrast to earlier hypotheses (Mjelde, 2004), shading or competition for nutrients by epiphytes seems not to hamper *J. bulbosus* nuisance growth. Our results are consistent with the results of Svedäng (1990), who suggested that *J. bulbosus* can avoid competition for CO_2 with epiphytic algae by using the relatively high CO_2 concentrations in early spring, when epiphytes are not yet present in large amounts.

We observed that at lake sites with low abundance of *J. bulbosus*, plant carbon content decreased from spring to autumn 2008, while in plants from high-abundance sites, it remained constant (Fig. 4c). This could indicate an autumn C-limitation in low-abundance lake sites, while we observed no such indications in high-abundance lakes. Likewise, water CO_2 concentration decreased from spring 2008 to summer 2010 in low-abundance lake sites, while it remained constant at high-abundance sites. This would be consistent with a summer CO_2 decline in low-abundance lakes but not in high-abundance lakes. These results both point towards a C-limitation of *J. bulbosus* in low-abundance lakes, while no such signs were

observed in high-abundance lakes, and no other factors except catchment slope are even close to being supported. These results are consistent with earlier studies which conclude that CO_2 is the most likely primary trigger for *J. bulbosus* nuisance growth in lakes (Roelofs et al., 1984). The probable cause for not observing enhanced CO_2 concentrations in high-abundance compared to low-abundance lakes is that the increase in CO_2 supply is small and has been assimilated into plant biomass. Moreover, *J. bulbosus* has been shown to be an effective user of sediment CO_2 (Wetzel et al., 1985), a parameter which we have not measured.

J. bulbosus surface mats were present in all investigated nuisance lakes, while not-nuisance lakes only rarely had surface mats. Wetzel et al. (1985) showed that CO_2 can diffuse via the internal lacunal airspace in *J. bulbosus*, such that CO_2 might be transported from the aerial leaves of surface mats to other plant parts. An uptake of aerial CO_2 and transport of C to other plant parts, either in form of CO_2 or carbohydrates, may therefore lead to increased *J. bulbosus* growth. It is interesting to note that such a mechanism would imply a positive feed-back, in very much the same way as we have argued above for NH_4^+ in rivers: the more plants have reached the water surface, the more CO_2 could be taken up through the aerial leaves, transported to other plant parts and support further growth. Other possible explanations for an enhanced CO_2 supply to *J. bulbosus* in high-abundance lakes include stimulated decomposition of organic sediment in formerly acidified lakes (van Kleef et al., 2010), enhanced production of CO_2 from DOC (Larsen et al., 2011b), and high spring CO_2 concentrations which can be effectively utilized by *J. bulbosus* (Svedäng, 1990).

The impact of catchment slope on *J. bulbosus* nuisance growth (Table 3) might also be connected to lake carbon metabolism. The ratio of sediment surface to lake volume, as well as lake area to lake volume, influences the fate of dissolved organic carbon and CO_2 export (Kelly et al., 2001; Flanagan and McCauley, 2008). Since we lack information about lake depth, volume and sediment surface, we cannot explicitly link catchment slope to these lake properties. *J. bulbosus* is, however, assumed to enhance C-recycling in the sediment (Chabbi, 1999), such that a lower rate of C-recycling in the water column, as described for deep lakes with a low ratio of sediment surface to lake volume (Kelly et al., 2001; Flanagan and McCauley, 2008), could give a competitive advantage to *J. bulbosus*.

Together, our results indicate that different primary triggers could indeed be responsible for *J. bulbosus* nuisance growth in rivers compared to lakes. Mass et al. (2010) investigated the influence of flow to marine benthic autotrophs and found that photosynthesis in flowing conditions is enhanced. They showed that this augmentation of photosynthesis is due to flow-

driven enhancement of oxygen efflux from the organism to the water, which increases the affinity of the RuBisCO enzyme to CO_2. Such a mechanism could physiologically explain a shift from C-limitation in lakes towards another nutrient in rivers and is consistent with our suggestion that C-availability is the most likely trigger for *J. bulbosus* nuisance growth in lakes, while NH_4^+ is primarily responsible in rivers.

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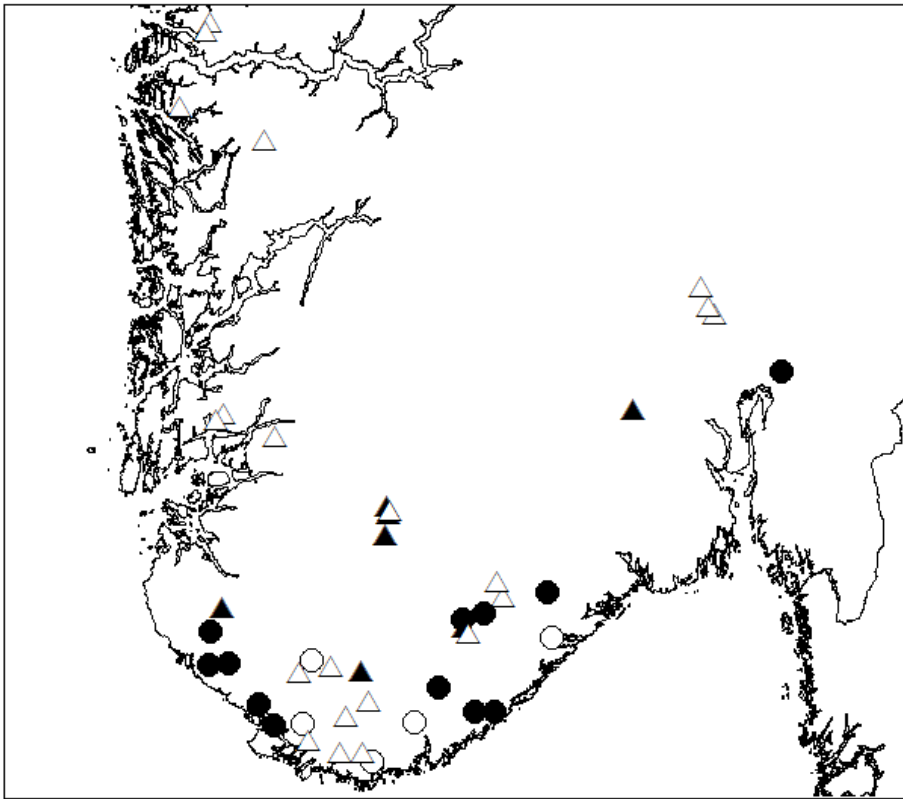
Fig. 1. Sampling sites in Southern Norway 2008 and 2010; circles represent lakes (n = 17), triangles river sites (n = 28). Black symbols represent sites with high abundance of *J. bulbosus*, white symbols sites with low abundance.
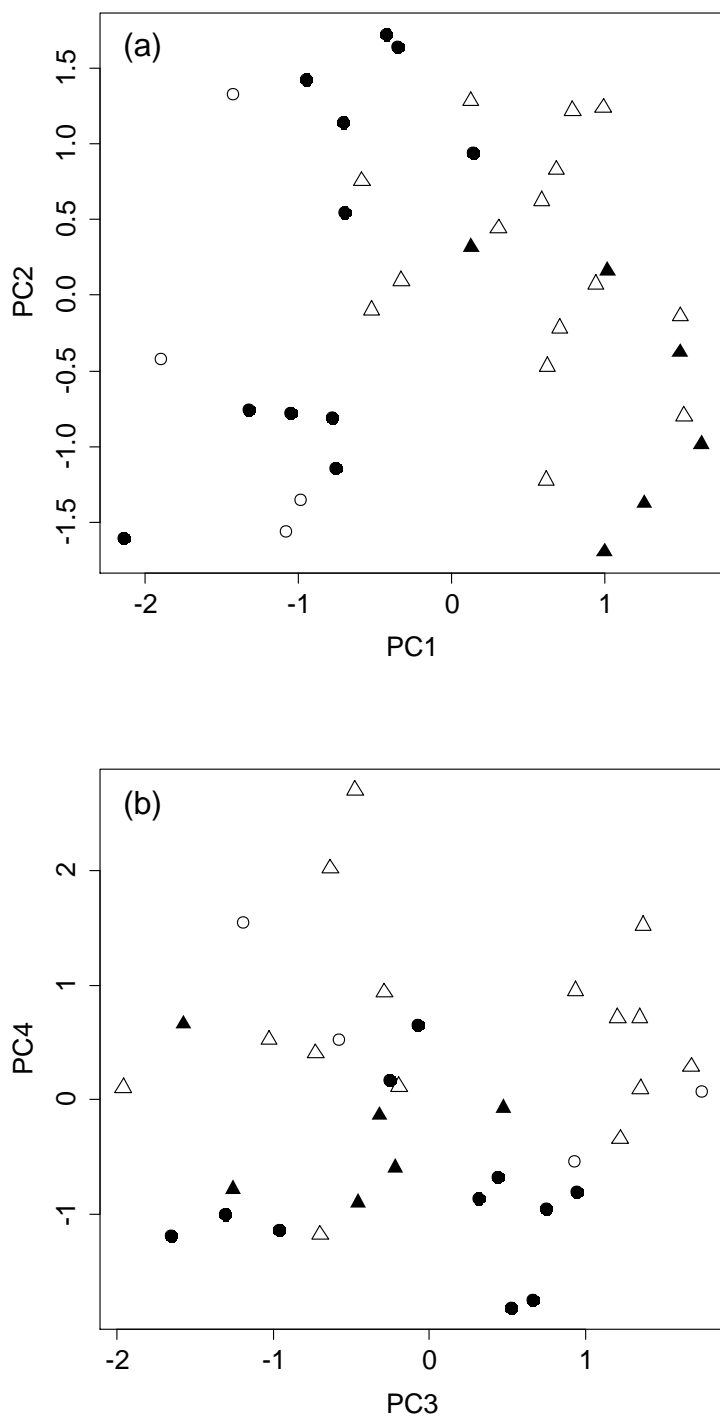
Fig. 2. Principal component analysis (PCA) of the pooled data from lakes and rivers; the components explained 25, 15, 15 and 9%, respectively, of the total variability. PC1 is mainly related to water conductivity, total nitrogen, sediment organic content and catchment variables, PC2 to water NO_3^- and sediment NH_4^+, PC3 to water phosphorus concentrations, precipitation and plant P and N content, while PC4 is mainly related to water pH and Ca-concentration (see Table 1 for details). Circles represent lakes, triangles river sites. Black

symbols represent sites with high abundance of *J. bulbosus*, white symbols sites with low abundance.
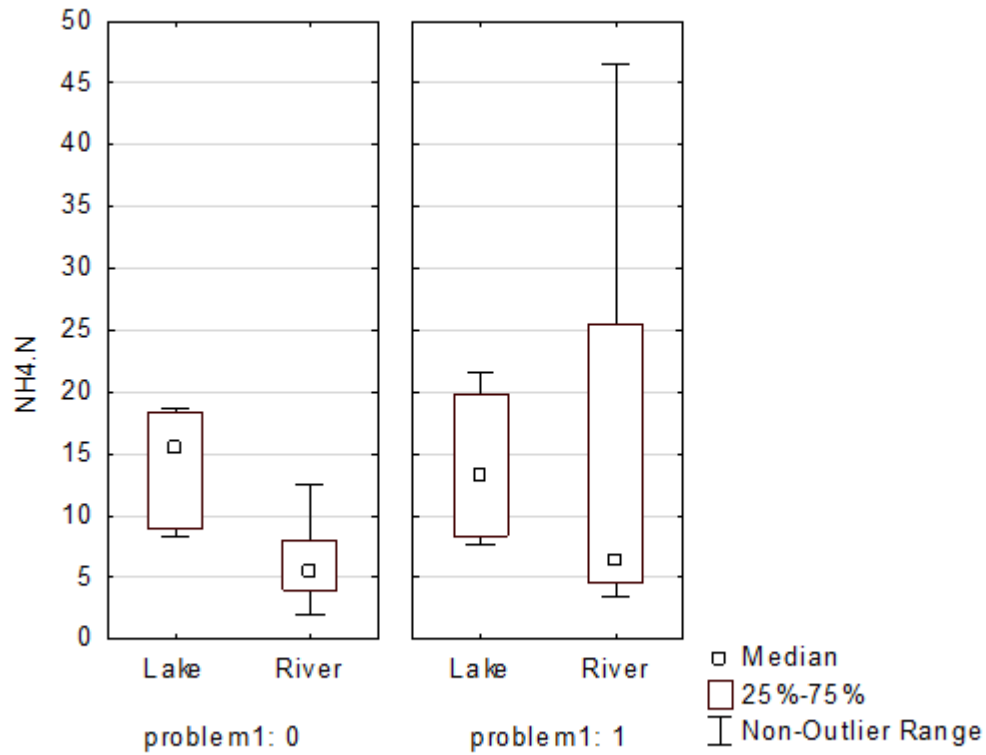
Fig. 3. Water NH_4^+-N concentrations (in $\mu g\ L^{-1}$) in rivers and lakes with high and low abundance of *J. bulbosus* in Southern Norway, using averages of samplings from 2008 and 2010. The difference between lakes and rivers is significant for low-abundance sites ($p = 0.001$), but not for high-abundance sites ($p = 0.34$).

2010 - 2008 sediment NH4

a)

2010 minus spring 2008 CO2

b)

autumn minus spring %C average total plant

c)
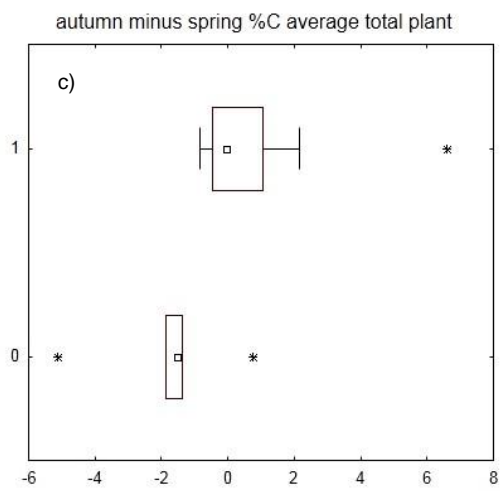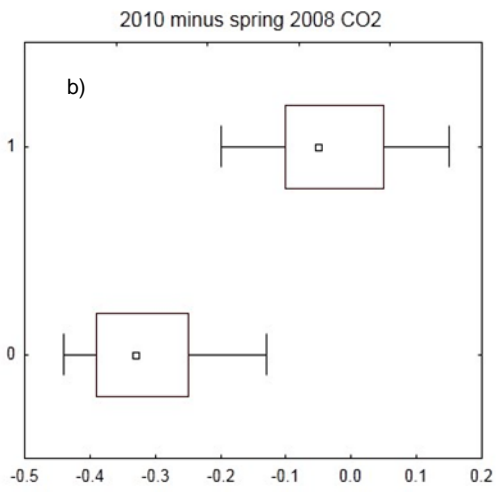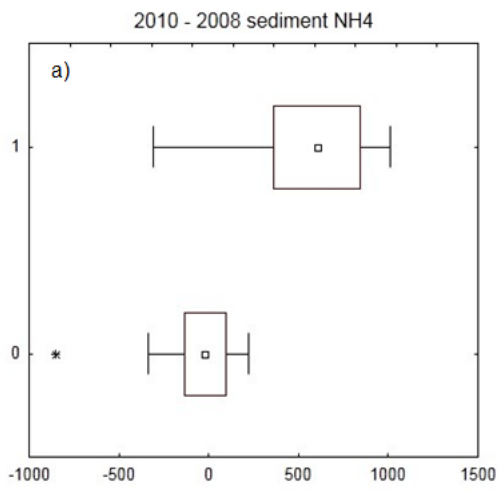
Fig. 4. a) change in river sediment NH_4^+-N content (in µg dm^{-3}) from 2008 to 2010; p = 0.046 for the difference between sites of high and low abundance of *J. bulbosus*; b) change in lake water CO_2 concentrations (in mg C L^{-1}) from spring 2008 to summer 2010 (p = 0.005), and (c) change in plant % C from spring to autumn 2008 (p = 0.031). 1 = high abundance of *J. bulbosus*, 0 = low abundance.

Table 1
Correlation of 39 parameters measured at 15 lake and 21 river sites with the first four components of a PCA. The components explained 25, 15, 15 and 9%, respectively, of the total variability. Correlations printed in bold are significant at p = 0.05.

	PC1	PC2	PC3	PC4
water chemistry				
pH	0.23	-0.14	-0.18	**0.71**
log conductivity	**-0.72**	0.27	0.22	0.24
log Ca	-0.26	-0.10	-0.17	**0.84**
log DIC	-0.22	**-0.63**	-0.17	**0.54**
log CO2	**-0.45**	**-0.53**	**-0.39**	0.04
log TOC	**-0.52**	**-0.60**	-0.09	0.16
TOTN	**-0.82**	0.05	-0.03	**0.35**
sqrt NO3-N	-0.19	**0.76**	-0.15	**0.39**
log NH4-N	**-0.42**	**-0.34**	-0.16	-0.23
log DIN	-0.24	**0.70**	-0.17	**0.36**
log TOTP	**-0.49**	**-0.57**	**0.45**	0.08
log PO4-P	**-0.35**	**-0.33**	**0.43**	0.32
sediment chemistry				
sqrt sediment water content	**-0.60**	**-0.33**	-0.03	**-0.46**
log sediment organic cont.	**-0.66**	**-0.44**	-0.04	**-0.36**
log pore water NH4-N	0.08	**-0.70**	0.11	-0.09
log sediment NH4-N	-0.18	**-0.77**	0.10	-0.29
log pore water PO4-P	0.09	-0.32	0.20	**0.53**
log sediment PO4-P	-0.21	**-0.52**	0.22	0.27
log pore water NO3-N	-0.15	**0.60**	0.09	0.22
log sediment NO3-N	**-0.41**	**0.41**	0.09	-0.02
catchment parameters				
log altitude	**0.90**	-0.18	-0.16	-0.05
log area	**0.75**	-0.14	-0.31	**0.37**
log runoff	**0.38**	0.32	**0.68**	-0.17
log N deposition	**-0.73**	0.18	0.05	-0.21
log NDVI	**-0.84**	0.16	-0.07	0.17
log slope	**0.66**	0.13	-0.27	-0.07
T.mean	**-0.84**	**0.37**	0.26	-0.02
log T.max	**-0.84**	0.03	-0.24	0.21
T.min	**-0.65**	**0.46**	**0.45**	-0.12
log precipitation	0.27	0.32	**0.71**	-0.20
plant parameters				
log %P average total plant	-0.11	-0.21	**0.59**	0.11
log %N average total plant	-0.08	0.03	**0.63**	0.02
%C average total plant	0.05	0.15	0.04	0.08
% P shoot	0.20	-0.09	**0.79**	0.17
% N shoot	**0.58**	-0.27	**0.49**	0.25
% C shoot	-0.28	-0.21	**0.38**	-0.28
C/N shoot	**-0.64**	0.14	**-0.47**	-0.23
C/P shoot	-0.25	0.05	**-0.85**	-0.19
N/P shoot	0.25	-0.04	**-0.77**	-0.08

Table 2

River water and sediment chemistry, catchment characteristics, presence of epiphytic algae, and plant CNP composition (21 river sites with low and 7 river sites with high abundance of *J. bulbosus*). Data are averaged from one measurement in 2008 and one in 2010; p-values < 0.05 (MWU-tests, Fisher's test for "weir basin") are marked in bold; NDVI = normalized difference vegetation index.

a) estimated as 1=low, 2=medium, 3=high velocity; b) estimated as 0=absent, 1=present; c) 0=not regulated, 0.5=min water flow, 1=full flow; d) 0=not limed, 0.5=indirect liming via inflows further upstream, 1=direct liming by dosers.

	unit	low abundance of *J. bulbosus*			p-value for difference between groups	high abundance of *J. bulbosus*		
		N	Mean	Std.Dev.		N	Mean	Std.Dev.
water chemistry								
pH	-	21	6.46	0.29	0.254	7	6.35	0.25
Conductivity	S m^{-1}	21	1.97E-03	8.52E-04	0.075	7	1.40E-03	5.69E-04
Ca	mg L^{-1}	21	1.50	0.63	0.075	7	1.09	0.56
DIC	mg L^{-1}	21	0.96	0.37	1.000	7	0.98	0.41
CO_2-C	mg L^{-1}	21	0.44	0.19	0.202	7	0.54	0.22
TOC	mg L^{-1}	21	2.84	1.18	0.193	7	2.41	1.19
TOTN	mg L^{-1}	21	0.237	0.064	0.265	7	0.203	0.063
NO3-N	mg L^{-1}	21	8.56E-02	5.89E-02	0.232	7	6.04E-02	7.78E-02
NH4-N	mg L^{-1}	21	5.98E-03	2.79E-03	0.202	7	1.52E-02	1.59E-02
DIN	mg L^{-1}	21	9.16E-02	5.92E-02	0.559	7	7.56E-02	7.40E-02
TOTP	mg L^{-1}	21	4.10E-03	1.56E-03	0.377	7	3.50E-03	1.73E-03
PO_4-P	mg L^{-1}	21	7.50E-04	3.35E-04	0.142	7	5.36E-04	9.45E-05
Velocity	a)	21	1.62	0.59	0.345	7	1.36	0.38
epiphytic algae								
filamentous algae	b)	21	0.10	0.30	0.843	7	0.07	0.19
small epiphytic algae	b)	21	0.40	0.44	0.113	7	0.71	0.39
sediment parameters								
Sediment water content	% of wet weight	16	38	15	0.060	6	50	14
Sediment organic cont.	% of dry weight	16	4.01	4.94	0.060	6	6.75	4.16
Pore water NH_4-N	mg L^{-1}	16	1.27	0.82	0.113	6	2.08	1.35
Sediment NH_4-N	g m^{-3}	16	0.513	0.510	**0.030**	6	1.06	0.64
Pore water PO_4-P	mg L^{-1}	16	0.026	0.027	0.083	6	0.010	0.005
Sediment PO_4-P	g m^{-3}	16	8.65E-03	8.34E-03	0.285	6	5.06E-03	2.71E-03
Pore water NO_3-N	mg L^{-1}	16	0.051	0.041	**0.014**	6	0.019	0.007
Sediment NO_3-N	g m^{-3}	16	0.017	0.012	0.113	6	0.008	0.003
catchment parameters								
Altitude	m	21	565	226	0.106	7	797	269
Catchment area	km^2	21	558	529	0.095	7	1439	1398
Runoff	mm year^{-1}	21	1803	960	0.474	7	1415	542
N deposition	mg m^{-2} year^{-1}	21	0.708	0.139	0.853	7	0.743	0.115
NDVI	index	21	131.1	8.8	0.106	7	124.9	8.2
Slope	degree	21	8.66	3.23	0.811	7	8.24	1.42
T.mean	°C	21	3.62	1.76	0.060	7	2.06	1.99
T.max	°C	21	15.44	1.63	0.095	7	14.21	1.30
T.min	°C	21	-6.39	3.36	0.145	7	-8.31	2.85
Precipitation	mm year^{-1}	21	1659	612	0.577	7	1482	306
regulation code	c)	21	0.5	0.5	0.353	7	0.7	0.4
weir basin	yes/no	21	0.1	0.3	0.253	7	0.3	0.5
liming code	d)	21	0.69	0.37	**0.021**	7	0.21	0.39
plant parameters								
% P root	% of dry weight	14	0.092	0.051	0.746	5	0.079	0.041
% N root	% of dry weight	18	1.34	0.36	0.301	6	1.51	0.37
% C root	% of dry weight	18	43.94	3.98	0.868	6	43.78	3.52
% P shoot	% of dry weight	20	0.172	0.079	0.194	7	0.129	0.052
% N shoot	% of dry weight	21	2.39	0.55	0.750	7	2.43	0.36
% C shoot	% of dry weight	21	42.80	2.50	1.000	7	42.47	1.33
%P average total plant	% of dry weight	21	0.171	0.084	0.124	7	0.123	0.048
%N average total plant	% of dry weight	21	1.76	0.41	0.367	7	1.55	0.29
%C average total plant	% of dry weight	21	46.96	1.14	0.340	7	46.52	1.64

Table 3
Lake water and sediment chemistry, catchment characteristics, presence of epiphytic algae, and plant CNP composition (5 lakes with low and 12 lakes with high *J. bulbosus* abundance). Data are averaged from two measurements in 2008 and one in 2010; p-values < 0.05 (MWU-tests) are marked in bold; NDVI = normalized difference vegetation index.
b) estimated as 0=absent, 1=present; d) 0=not limed, 0.5=indirect liming via inflows further upstream, 1=direct lime application.

	unit	N	low abundance of *J. bulbosus* Mean	Std.Dev.	p-value for difference between groups	N	high abundance of *J. bulbosus* Mean	Std.Dev.
water chemistry								
pH	-	5	6.01	0.70	0.635	12	5.96	0.43
Conductivity	$S\ m^{-1}$	5	4.0E-03	2.0E-03	0.429	12	3.0E-03	1.0E-03
Ca	$mg\ L^{-1}$	5	1.62	1.27	0.317	12	1.05	0.57
DIC	$mg\ L^{-1}$	5	0.97	0.41	0.712	12	0.88	0.39
CO_2-C	$mg\ L^{-1}$	5	0.71	0.29	0.712	12	0.64	0.20
TOC	$mg\ L^{-1}$	5	4.57	2.06	0.493	12	3.69	2.49
TOTN	$mg\ L^{-1}$	5	0.36	0.04	0.126	12	0.300	0.075
NO_3-N	$mg\ L^{-1}$	5	0.116	0.108	0.752	12	0.089	0.082
NH_4-N	$mg\ L^{-1}$	5	1.40E-02	5.01E-03	1.000	12	1.39E-02	5.89E-03
DIN	$mg\ L^{-1}$	5	0.130	0.108	0.958	12	0.103	0.078
TOTP	$mg\ L^{-1}$	5	8.67E-03	7.07E-03	0.597	12	5.44E-03	2.76E-03
PO_4-P	$mg\ L^{-1}$	5	1.60E-03	1.53E-03	0.170	12	6.25E-04	1.76E-04
Secchi depth	m	5	4.9	3.2	0.955	11	5.8	4.8
vegetation parameters								
filamentous algae	b)	5	0.20	0.30	0.952	12	0.19	0.26
small epiphytic algae	b)	5	0.60	0.43	1.000	12	0.61	0.31
max. vegetation depth	m	5	3.5	1.0	0.748	12	3.6	1.4
total abundance isoetids	sum of abund.	5	6.3	1.5	0.313	12	4.9	2.3
sediment parameters								
Sediment water content	% of wet weight	5	68	22	0.712	12	72	20
Sediment organic cont.	% of dry weight	5	17.74	11.57	0.562	12	27.90	23.43
Pore water NH_4-N	$mg\ L^{-1}$	5	1.29	1.22	0.792	12	2.17	3.40
Sediment NH_4-N	$g\ m^{-3}$	5	0.919	0.902	0.562	12	1.629	2.640
Pore water PO_4-P	$mg\ L^{-1}$	5	0.014	0.009	0.792	12	0.02	0.02
Sediment PO_4-P	$g\ m^{-3}$	5	0.010	0.007	0.874	12	0.012	0.015
Pore water NO_3-N	$mg\ L^{-1}$	5	0.034	0.020	0.792	12	0.088	0.173
Sediment NO_3-N	$g\ m^{-3}$	5	0.021	0.012	0.874	12	0.075	0.158
catchment parameters								
Altitude	m	5	223.0	92.2	0.317	12	278.0	127.9
Catchment area	km^2	5	6.7	6.8	0.958	12	17.8	45.3
Runoff	$mm\ year^{-1}$	5	1114	397	0.792	12	1230	423
N deposition	$mg\ m^{-2}\ year^{-1}$	5	0.96	0.05	0.073	12	0.90	0.07
NDVI	index	5	142.1	6.0	0.317	12	138.7	4.3
Slope	degree	5	2.88	1.01	**0.018**	12	5.99	2.86
Solar irradiation	$W\ m^{-2}$	5	8.9E-10	1.30E-11	0.188	12	8.80E-10	1.00E-11
UVA	$J\ m^{-2}$	5	2.E+08	7.E+06	0.712	12	2.E+08	6.E+06
T.mean	^{o}C	5	5.92	0.68	0.370	12	5.55	0.85
T.max	^{o}C	5	16.91	1.32	0.958	12	17.02	1.28
T.min	^{o}C	5	-3.90	0.76	0.958	12	-4.60	1.88
Precipitation	$mm\ year^{-1}$	5	1424	330	0.874	12	1369	354
liming code	d)	5	0.10	0.22	1.000	12	0.13	0.23
plant parameters								
% P root	% of dry weight	3	0.07	0.04	0.699	6	0.11	0.08
% N root	% of dry weight	5	1.22	0.47	0.626	7	1.02	0.17
% C root	% of dry weight	5	42.03	4.52	0.516	7	43.49	3.37
% P shoot	% of dry weight	4	0.13	0.07	0.744	11	0.12	0.05
% N shoot	% of dry weight	5	1.87	0.62	0.821	11	1.71	0.35
% C shoot	% of dry weight	5	42.81	0.89	0.113	11	43.64	1.19
%P average total plant	% of dry weight	5	0.17	0.07	0.429	12	0.14	0.05
%N average total plant	% of dry weight	5	1.70	0.13	0.429	12	1.63	0.14
%C average total plant	% of dry weight	5	45.96	1.31	0.268	12	46.87	0.96

Table 4
P-values for differences between rivers and lakes (averaged from 2008 and 2010 measurements), divided into sites with high and low *J. bulbosus* abundance. All water and sediment chemical variables given in Tables 1 and 2, as well as plant elemental compositions were tested; here we only show variables where p-values are < 0.05 (MWU-tests) at either nuisance or not-nuisance growth (marked in bold).

	low abundance of *J. bulbosus*			high abundance *of J. bulbosus*		
	p-value for difference between rivers and lakes	median value lakes	median value rivers	p-value for difference between rivers and lakes	median value lakes	median value rivers
pH	0.200	6.19	6.48	**0.045**	5.93	6.37
conductivity	**0.003**	3.32	1.68	**0.003**	3.17	1.24
surface water TOTN	**0.001**	380.0	257.5	**0.017**	300.0	195.0
surface water NH4-N	**0.001**	15.67	5.50	0.340	13.33	6.50
Sediment water content	**0.019**	0.73	0.34	**0.032**	0.81	0.48
Sediment organic content	**0.004**	17.42	2.36	**0.041**	17.23	6.28
% N shoot	**0.034**	1.59	2.30	**0.000**	1.75	2.36