PRIMARY RESEARCH PAPER

Direct and indirect effects of salinisation on riverine biota: a case study from river Wipper, Germany

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Abstract Salinisation has direct and detrimental physiological effects on freshwater organisms, yet little is known about its indirect effects. Here, we present a study that investigated the primary and secondary effects of salinisation on aquatic macroinvertebrates. We analysed macroinvertebrate samples from nine sites in river Wipper, Germany against nine stressor variables (water quality, salinisation, hydromorphological degradation). A Principal Component Analysis showed water quality deterioration and physical habitat degradation to constitute the main stressor gradients. Two macroinvertebrate community metrics (index of general degradation and percent Ephemeroptera-Plecoptera-Trichoptera specimens) revealed strong and significant positive correlations with water quality, but only weak and insignificant positive correlations with hydromorphological quality. High-resolution temporal measurements revealed notable oxygen deficits at a salinised and macrophyte-rich site that was dominated by the salt-tolerant macrophyte species *Stuckenia* [*Potamogeton*] *pectinata* (L.) Börner. At the site, oxygen levels frequently dropped below 6 mg/L during nighttime, suggesting an interaction of osmoregulatory stress (through salinisation) and respiratory stress (through plant mitochondrial respiration) that is caused by the mass development of a salt-tolerant macrophyte species. This biologically driven interaction of direct and indirect salinisation effects adds another level of complexity to the influence of multiple stressors in lotic systems and requires consideration in river management and restoration.

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Introduction

Salinisation of terrestrial and freshwater ecosystems is considered an emerging stressor (Kaushal et al., 2021), last but not least due to its connection

with global and climate change (De Castro-Català et al., 2015). In semi-arid regions, crop production often requires intense irrigation, which can foster soil salinisation (Schuler et al., 2018) and then may impose negative effects on streams and rivers. With global warming, the thirst for irrigation water is likely to increase also in temperate regions. Large parts of central Europe, for example, witnessed extremely dry spring seasons between 2007 and 2020 (Ionita et al., 2020). The ten hottest summers in Europe have all occurred since 2003 (Copernicus, 2022). Hence, both global warming and a higher probability of extreme drought events are likely to put freshwater ecosystems further at risk.

Besides irrigation, the production and application of fertilizers—namely potash (potassium chloride, KCl)—constitutes another important source of salinisation (Cañedo-Argüelles et al., 2018; Schulz & Cañedo-Argüelles, 2018). Potash is a natural mineral usually obtained by underground mining. However, it is only the potassium ion (but not chloride) that renders potash an invaluable fertiliser, because potassium has been found to enhance the stress tolerance of many agricultural crops such as corn, wheat and rye (Wang et al., 2013). Manufacturing potassium fertilisers from salt rocks gives rise to considerable amounts of residues often containing several non-targeted salt ions (e g., chloride, sodium, sulphate). These residues are treated as waste and are usually dumped, for example, as open solid stock piles. Being exposed to precipitation, the salt is quickly dissolved, which renders open stock piles and their drainage a considerable source of brine. Disposal of brine into rivers usually has severe adverse effects on the riverine biodiversity (Cañedo-Argüelles et al., 2013; Kefford et al., 2016).

From an organismal perspective, salt ions are directly operating and physiologically highly active and hence may impose immediate osmoregulatory stress on many freshwater organisms, including aquatic macrophytes, macroinvertebrates and fish (Beisel et al., 2011). The stress level is dependent on the overall concentration of salt ions (i.e., the level of salinisation), but also on the composition of particular ions. Anions such as chloride (Cl^-) and sulphate (SO_4^{--}) have been found to impose higher stress levels as compared to cations such as potassium (K^+), calcium (Ca^{++}) and magnesium (Mg^{++}) (Ziemann, 1967; Schuler et al., 2018). Halse et al.

(2003) reported a strong, non-linear decline of macroinvertebrate richness under moderate levels of chloride, whereas recent studies from Germany imply the loss of many EPT (Ephemeroptera, Plecoptera and Trichoptera) taxa at chloride levels as low as 30–50 mg/L (Sundermann, 2015; Halle et al., 2017). For sulphate, Simmons (2012) found highly toxic effects on the duckweed *Lemna minor* L., which, however, were different in the presence of sodium and potassium. While sodium increased the toxicity of sulphate (supplied as Na_2SO_4), the presence of potassium and calcium enhanced the duckweed's tolerance to sodium sulphate. A similar protective effect of calcium has been reported by Nanjappa et al. (2022) for the mayfly *Austrophlebioides* sp. AV2 Campbell & Suter. While sodium sulphate turned out to be most toxic, potassium chloride (KCl), calcium chloride ($CaCl_2$) and potassium sulphate (K_2SO_4) were least toxic. These examples imply beneficial effects of several cations (but not sodium) on the salt tolerance of aquatic plants (Rout & Shaw, 2001). In contrast a review by Griffith (2016), which addressed the osmoregulatory and ionoregulatory effects of several major salt ions and estimated their toxicity for freshwater fish, arthropods and molluscs, concluded that potassium appeared to have the highest potential for causing toxic effects to freshwater animals under high concentrations in the water.

Besides salinisation levels and the particular ion's identity, the biological response to salinisation is dependent on the osmoregulatory ability of particular species and species groups. The capability to control and regulate the inner osmolarity is well pronounced, for example, for many freshwater fish, but less so for freshwater plants and macroinvertebrates (Beisel et al., 2011; Wolfram et al., 2014). Therefore, salinisation can have immediate adverse effects on freshwater biodiversity and ecosystem functioning (Cañedo-Argüelles et al., 2013, 2018), especially among those species groups that lack a pronounced osmoregulatory capability. This is supported by the low tolerance of many riverine EPT taxa (Sundermann, 2015; Halle et al., 2017), which contribute notably to riverine macroinvertebrate biodiversity as well as to ecosystem functions such as organic matter decomposition (Wallace & Webster, 1996).

While the immediate and direct osmoregulatory effects of salinisation on freshwater organisms are well reported (Beisel et al., 2011; Silver & Donini,

2021, see also Cunillera-Montcusi et al., 2022 for a review), little is known about potential indirect effects. Personal observations from river Wipper in Thuringia, Germany, for example, suggest a boost of salt-tolerant macrophytes, namely *Stuckenia pectinata* (L.) Börner in heavily salinised sections of the river (up to 1500 mg/L chloride). There, the plant's respiration during nighttime may impose additional respiratory stress on breathing organisms such as macroinvertebrates or fish. Following this causal inference, salinisation would indirectly cause oxygen depletion, with primary production being the potential link between primary and secondary effects. Here, we present a study that was driven by the attempt to disentangle the causes of degradation of benthic macroinvertebrate communities in the brine-loaded catchment of river Wipper, Thuringia, Germany. In particular, we investigated the role of salinisation (cations and anions) originating from potash mining and tried to disentangle the potential link between direct (osmoregulatory) and indirect (macrophyte-driven respiratory) effects of salinisation on macroinvertebrates.

Material and methods

Study area

River Wipper is located south of the mountain range 'Hainleite' in Thuringia, Germany (Fig. 1). Its 92 km long course between the source at the city of Worbis in the west (330 m a.s.l.) and the mouth (into river Unstrut) at the city of Sachsenburg in the east (142 m a.s.l.) is characterised by calcareous minerals. Due to the calcareous geology, three different stream types can be found according to Pottgiesser (2018); type 6 (small fine substrate-dominated calcareous highland rivers), type 7 (small coarse substrate-dominated calcareous highland rivers) and type 9.1 (mid-sized fine to coarse substrate-dominated calcareous highland rivers). The carbonatic character of the catchment is distinctly pronounced by several salt springs at the river bottom. These springs constitute a natural source of salinisation, yet with much lower concentrations of salt ions as compared to the brine (Sommer et al., 2012). Because of the lack of sound data on natural salinisation, both natural and mining-related salinisation were not separated in

this study. The 647 km² catchment predominantly drains agricultural land (crops, pastures, meadows), with only a small proportion of forests and a few small cities located along the river course, of which Sondershausen is the biggest one (approx. 21,000 inhabitants).

Due to intensive potash mining activities between the 1890s and 1990s along the middle part of the Wipper and one of its tributaries, river Bode, large parts of the Wipper system continue to be impacted by salinisation, with chloride concentrations exceeding 1500 mg/L at Hachelbich in the lower part of the catchment (Fig. 1). In addition to chloride, the main salt ions include sulphate, sodium, magnesium, calcium and potassium, the latter of which is the target ion for the production of potash fertiliser (KCl). For decades, non-targeted production residues were dumped at four dumps close to the rivers Wipper and Bode and since then act as a constant donor of brine. If mobilised by rainwater, the salt enters the Wipper system either through surface runoff or through groundwater infiltration. Moreover, brine from three dumps is stored in a retention basin and released to the lower Wipper depending on the river's discharge. This constant pollution by salt has turned large parts of the Wipper into a degraded river system of poor to bad ecological status according to the WFD assessment (Fig. 1).

Data sources

Abiotic monitoring data of the Wipper

The following physical water quality variables were measured in the field using field probes, either in parallel or shortly before biological sampling in late spring 2016: electric conductivity (LF 196, WTW company Weilheim, Germany), pH (inoLab, WTW company Weilheim, Germany), oxygen concentration (Oxi 330, WTW company Weilheim, Germany) and water temperature (LF 196, WTW company Weilheim, Germany). In parallel to physical measurements, a water sample (1 L) was taken and kept cool for transport to the lab, where chemical analysis took place according to national standards. Lab analysis of chemical variables encompassed salt ions (chloride, sulphate, magnesium, calcium, sodium, potassium), nitrogen components (ammonia nitrogen, nitrate
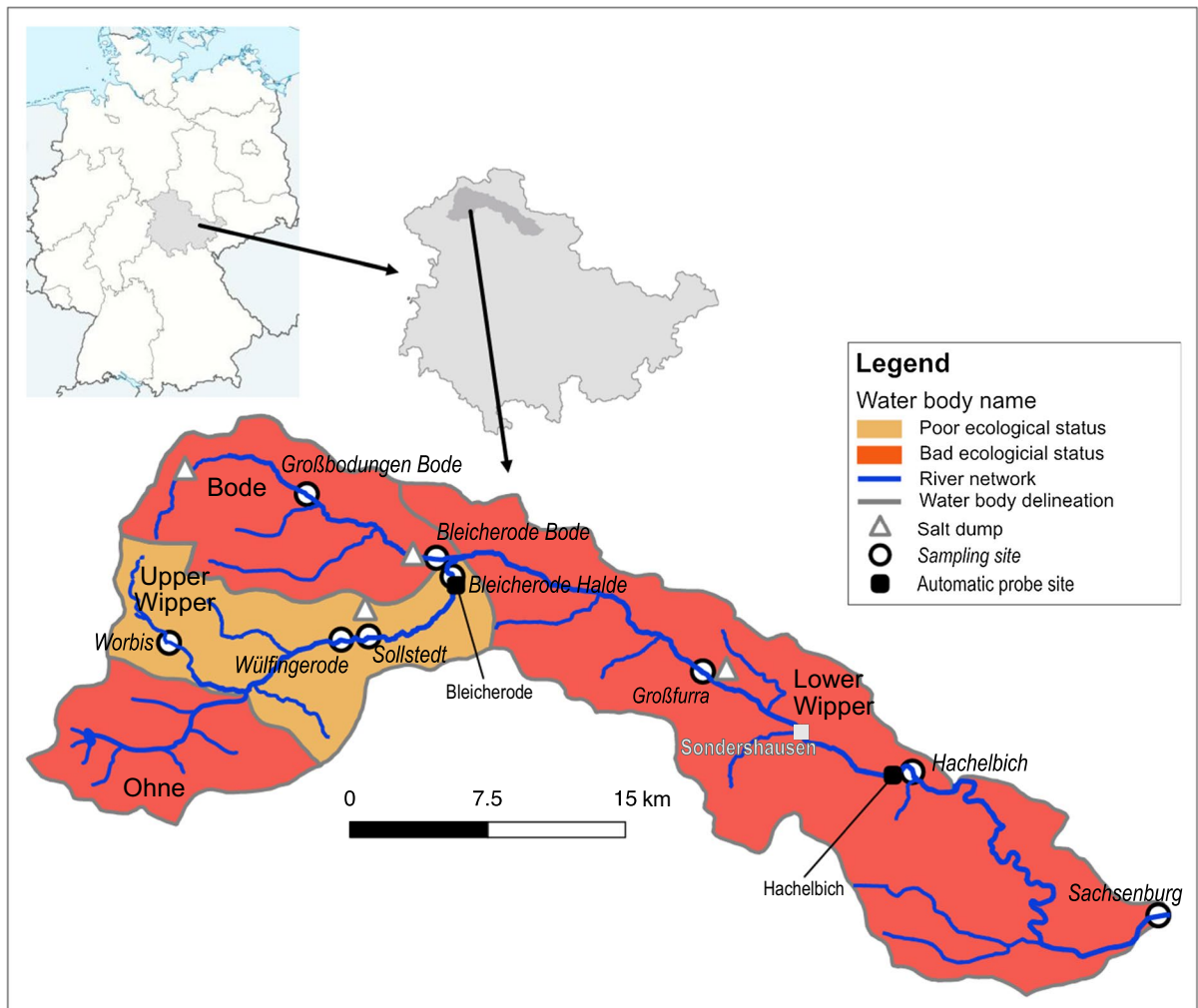
Fig. 1 Map of the Wipper basin with location of sampling sites

nitrogen) and phosphorous components (ortho-phosphate phosphorus, total phosphorus).

Fifteen physical habitat variables including hydrological (e.g., stagnation, presence of weirs/dams), morphological (e.g., bottom substrate conditions and diversity, bank modifications and special features) and riparian conditions were also recorded in the field in 2013 at the scale of 100 m intervals. For each interval, physical habitat variables were summarised in a physical habitat quality index (Gellert et al., 2014). For our analyses, only those 100 m river sections were considered that also included biological sampling sites. Because the physical habitat structure of the Wipper remained relatively

stable in the past decade (no major modification like flood protection or restoration measures took place), the physical habitat data from 2013 are considered comparable with the data obtained in 2016.

Catchment land use/cover of biological sampling sites was determined by clipping ATKIS land cover data (ADV, 2021) with polygons of each site's individual catchment using a Geographical Information System (GIS). Four land use/cover categories were distinguished: forest, grassland, crop and urban area. Other categories (e.g., surface waters, industrial areas) made up less than one percent coverage of the site's catchment and thus were excluded from the analysis.

High-resolution abiotic measurements along the Wipper

At two sites (Fig. 1), automatic probes were installed to measure physical and chemical parameters online at a temporal resolution of 15-min intervals (except P_{total}: 60 min; Table 3). This allowed for a detailed comparison of physical and chemical conditions under the influence of brine. The site at Bleicherode was located close to the biological sampling site 'Bleicherode Halde' in the Wipper upstream of its confluence with river Bode. The site was moderately impacted by brine discharge. In contrast, the site at Hachelbich was located further downstream, close to the biological sampling site 'Hachelbich' (Fig. 1) and severely impacted by brine discharge. Online measurement ran from April 1st until October 31st, 2016. Prior to statistical analysis, non-plausible extreme measurements (e.g., due to malfunction of probes) were identified as lying outside the interval [25th quantile–1.5-fold interquartile range, 75th quantile + 1.5-fold interquartile range] and removed from the dataset. Unreliable values (e.g., data gaps and zero-values recorded during and shortly before/after several maintenance events) were graphically identified and removed from the dataset.

To enable separate statistics for daytime and nighttime measurements, data/time stamps of individual measurements were linked to daily sunrise/sunset times using the R package 'photobiology' (Aphalo, 2015), with time zone set to Europe/Berlin and longitude/latitude set to the city of Bleicherode (Fig. 1). Daytime (as the estimated start of daily primary production) was set to sunrise plus one hour, while nighttime start was set to sunset as the expected daily end of the photoperiod.

Biological monitoring data at the Wipper

Biological sampling was conducted at nine sites (Fig. 1) between April and August 2016. Macrophyte sampling followed the German standard protocol (Schaumburg et al., 2004), with in situ identification of all macrophyte species within a sampling stretch of 50 m and estimations of each species' abundance according to Kohler (1978). Kohler's abundance classes (1 = very rare … 5 = very abundant/mass development) were transferred to percent coverage according to Londo (1974) (1: < 1%, 2: 1–5%,

3: > 5–25%, 4: > 25–50%, 5: > 50–100%). Macrophyte taxalists were assessed with the German standard assessment system Phylib v5.3 (Schaumburg et al., 2012).

Macroinvertebrate sampling followed the German standard protocol 'Perlodes' (Meier et al., 2006), which is based on multi-habitat sampling (Hering et al., 2004). At each site, within a sampling stretch of 50–100 m, bottom substrate cover was estimated at 5% increments. A total of 20 sub-samples (20 × 5% = 100%) were then allocated according to the individual substrate's bottom cover. For example, a substrate covering 30% of the bottom would be assigned six sub-samples. Sub-samples were taken with a kick-net (25 × 25 cm, mesh: 500 μm) that was placed on the bottom, while the substrate in front of the net was disturbed (by hand or heel) to move disclosed macroinvertebrates into the net. All sub-samples were then pooled, transferred into a container and fixed with ethanol (final concentration: 70%) prior to lab transport. Samples were stored at 4 °C in the dark in a refrigerator until further processing. Representative sub-samples comprising at least a sixth of the pooled sampling material and 350 macroinvertebrate specimens were taken from each pooled sample and sorted. After sorting, macroinvertebrates were identified to the taxon levels as defined by the operational taxalist (Haase et al., 2019), which is species level except for oligochaetes (worms) and dipterans (flies, midges). Eventually, macroinvertebrate taxalists were processed with the software ASTERICS v4.04 (ASTERICS, 2014) to obtain (i) the overall ecological status class (ECS), (ii) the ecological quality ratio (EQR) of the module 'General Degradation', which assesses the physical habitat quality (AD_EQR), and (iii) the ecological quality ratio of the proportion of EPT specimens in the community (EPT_EQR). EQRs are calculated by dividing the observed value by a stream type-specific expected value (O/E ratio). For a detailed description of the metrics, see Schaumburg et al. (2012) and Meier et al. (2006).

Additional monitoring data of further German rivers

Due to the low number of available monitoring sites in the Wipper system, additional monitoring data from other watersheds in Germany were analysed to verify the results based upon the Wipper data. The dataset comprised macrophyte coverages and salt ions from 60

observations at 39 rivers of comparable stream types (type 6, 7 and 9.1 acc. to Pottgiesser, 2018), to ensure that the natural geo-morphological background conditions of the verification sites matched those in the Wipper. Sampling of biological and abiotic data of the verification dataset followed the same protocols as outlined above for the Wipper monitoring dataset.

Statistical analysis

All statistical analyses and graphical representations of results were obtained with R v4.0.5 (R Core Team, 2021). Statistical significance of observed differences between groups of sites were analysed using the Mann–Whitney *U*-test (function `wilcox.test()`) with the minimum type-I error set to $P < 0.05$, however, significant results could not be obtained due to the small sample size.

Because of the limited sample size, regression modelling (e.g., GLM) seemed inappropriate to derive the stressor hierarchy from the Wipper data. Therefore, we chose a combination of Principal Components Analysis (PCA) and subsequent correlation with the main PCA components to compare the relationship of stressor variables and macroinvertebrate metrics. First, physical, chemical, and physical habitat stressors were subjected to a variance inflation factor (VIF) analysis (package `usdm`; Naimi et al., 2014), to identify non-collinear stressor variables. Stressor variables with a VIF > 10 (Dormann et al., 2012) were excluded from further analyses. Also, land use variables were excluded, because they revealed largely similar (i.e., invariable) values at all sites. Second, a PCA using the function `princomp()` and a correlation matrix was run with five non-collinear stressor variables, to identify the main stressor gradients. And third, the relationship between the main PCA components and the two macroinvertebrate metrics was investigated using Spearman's correlation coefficient ρ, to quantify the relationship. Correlations were tested for significance with R's function `cor.test()`.

Results

Ecological status of the Wipper system

Environmental monitoring revealed that the Wipper system is heavily impacted by several stressors

(Table 1). Stressor levels not meeting the national or other published quality targets show strong impacts by nutrient enrichment, salinisation, physical habitat modification and land use. While nutrient enrichment was moderate, stressors of the remaining three categories (salinisation, physical habitat modification and land use) exceeded quality targets manifold.

Ecological quality ratios (EQR) of macrophytes and macroinvertebrates along the river continuum confirm pronounced ecological implications in the lower Wipper, which could be attributed mainly to water and habitat quality issues (Fig. 2). Water quality in the lower Wipper was predominantly deteriorated by enhanced concentrations of chloride, sulphate and potassium. The (daytime) oxygen deficits at Großfurra and Hachelbich (Fig. 2), together with rather inconsistent trends in ammonia, nitrate and orthophosphate along the continuum suggest interactions of physical and chemical stressors with macrophytes (mainly *S. pectinata*) and benthic algae [mainly *Cladophora glomerata* (L.) Kütz and *Enteromorpha intestinalis* (L.) Nees].

### Effects of water and habitat quality on macrophytes

The comparison of stressor levels in macrophyte-poor (upstream) and macrophyte-rich (downstream) river sites shows mainly water quality variables to distinguish between both sections (Table 2), whereas differences in physical habitat quality and land use were less pronounced (see also Fig. S1 in the Supplementary Material for a comparison of salt *vs.* habitat as descriptors of macrophyte coverage). Nitrate dropped from levels above 5 mg/L at the sites upstream of Großfurra, to levels ranging 2–3 mg/L further downstream, thus implying an uptake of nitrate due to primary production. The levels of ammonia, ortho-phosphate and total phosphorus, however, were at least doubled in the lower Wipper and suggest the presence of active sources of pollution along the river continuum (see also Fig. 2), rather than an interaction with macrophytes. Macrophyte-rich sites were also characterised by warmer water, which – in part – may point at a stronger solar heating under reduced flow conditions in dense macrophyte stands. Yet, the warming of streams along the continuum in general is a natural phenomenon, which is difficult to disentangle from other (anthropogenic) causes of heating due to the lack of sufficient data in this study.

Table 1 Overview of the stressors operating in the Wipper basin at the time of biological sampling in 2016 (for site names/codes, see Fig. 1)

Parameter group	Parameter (quality target)	Worbis	Wülfingerode	Sollstedt	Bleicherode Halde	Großbodungen	Bleicherode Bode	Großfurra	Hachelbich	Sachsenburg
	River name	Wipper	Wipper	Wipper	Wipper	Bode	Bode	Wipper	Wipper	Wipper
Physical	O_2 ($\leq$7 mg/L)[1]	10	10.6	12	10.3	13.3	10.9	**6.81**	**5.45**	7.97
	pH (7–8.5)[2]	8.29	8.2	8.38	8.18	8.42	8.17	7.99	7.78	8.19
	Electr. conductivity (µS/cm)[1]	766	1070	1160	1890	3390	2160	5430	5000	4410
	T_{water} (°C)	10.6	10.7	9.1	9.6	8.5	9.4	16.8	15.4	17.1
Nutrients	NH_4-N ($\leq$0.1 mg/L)[1]	0.015	0.038	0.015	0.015	0.015	0.015	0.032	**0.177**	0.015
	NO_3-N ($\leq$5 mg/L)[3]	**5.823**	**5.365**	**5.274**	**5.417**	4.51	**5.092**	2.14	2.789	1.935
	o-PO_4-P ($\leq$0.07 mg/L)[1]	0.01	**0.135**	0.053	0.031	0.01	0.03	**0.136**	**0.105**	**0.129**
	P_{tot} ($\leq$0.1 mg/L)[1]	0.022	**0.244**	**0.107**	0.086	0.01	0.076	**0.249**	**0.287**	**0.221**
Salt	Cl ($\leq$200 mg/L)[1]	46	85	123	**338**	**824**	**408**	**1490**	**1480**	**1050**
	SO_4 ($\leq$220 mg/L)[1]	98	193	169	**250**	**254**	**267**	**363**	**304**	**496**
	K ($\leq$5 mg/L)[4]	4.5	**6.8**	**11**	**19.5**	**46.8**	**25.5**	**74.7**	**77**	**56.9**
	Na (26–50 mg/L)[4]	10	**50**	**72**	**136**	**355**	**171**	**698**	**658**	**466**
	Mg (31.5–38 mg/L)[4]	22	26	23	42	**66**	**50**	**100**	**110**	**105**
	Ca (140–165 mg/L)[4]	133	161	145	**192**	**244**	**197**	**250**	**237**	**274**
Physical habitat	Habitat index ($\leq$3.5)[5]	**7**	**5**	**4**	3	**4**	**7**	**5**	**5**	**6**
	Macrophyte cover (%)	5	0	15	0	NA	NA	50	40	100
	Algal cover (%)	0	90	75	0	NA	NA	50	40	0
Catchment land use	Crop land (30–50%)[6]	**52.6**	**68.7**	**77.9**	**75.4**	NA	NA	**98**	**43.8**	**92.4**
	Grassland (%)	1.3	7.7	1.6	8.4	NA	NA	0.7	12.5	1.3
	Urban (8–12%)[6]	5.8	2.4	5.3	1.7	NA	NA	0.2	5.6	0.2
	Forest (%)	40.3	21	15.1	14.3	NA	NA	1.1	37.7	6.2

[1] Minimum value as arithmetic mean of annual minima values from a maximum period of three consecutive years (acc. to OGewV, 2016)

[2] Annual arithmetic mean value within range of annual minima/maxima from a maximum period of three consecutive years (acc. to OGewV, 2016)

[3] Annual mean value based upon $\geq$4 single measurements during the year acc. to Halle and Müller (2014)

[4] Annual mean value based upon $\geq$4 single measurements during the year acc. to Halle and Müller (2015)

[5] Thuringian quality target value (TLUG, 2011)

[6] Proposed target value acc. to Allan (2004)

Stressor levels exceeding national or other published quality targets are indicated in bold

NA data not available
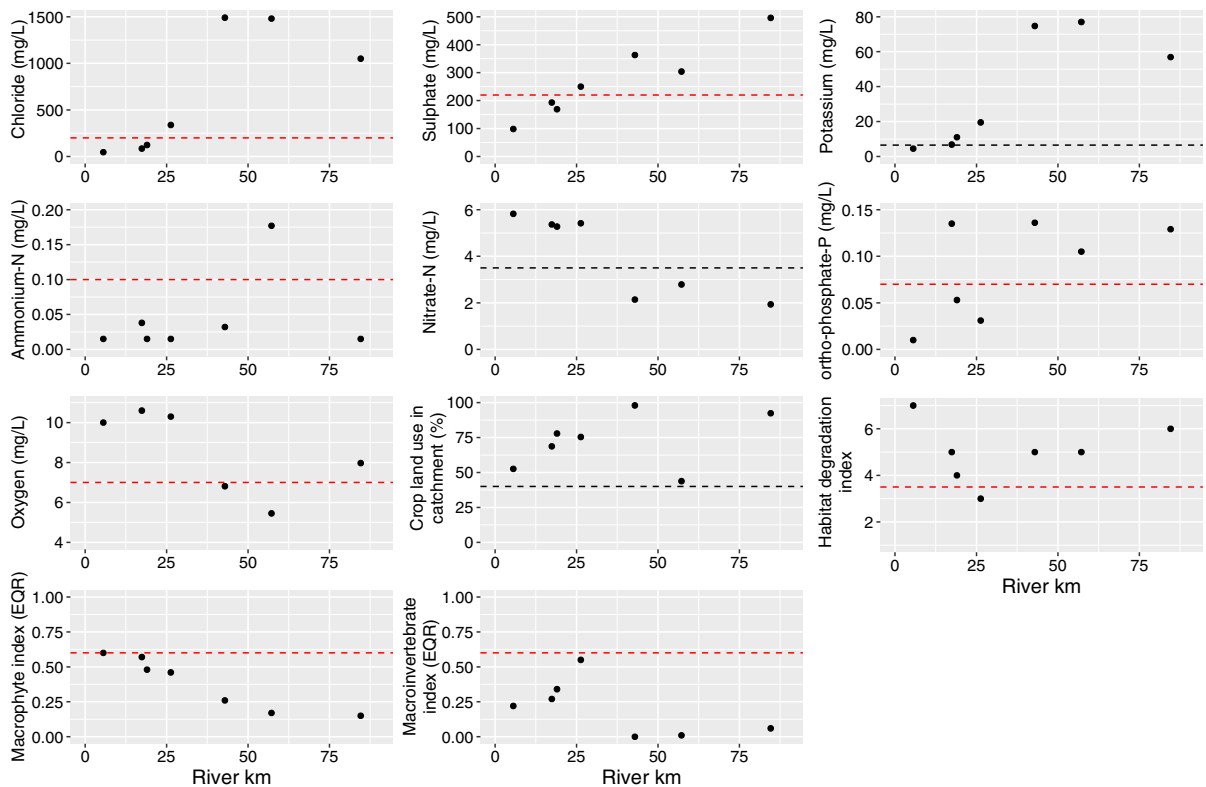
Fig. 2 Nine stressor variables and two biological indices at seven sites (black dots) along the Wipper continuum. Sites are (from left to right): Worbis, Wülfingerode, Sollstedt, Bleicherode Halde, Großfurra, Hachelbich and Sachsenburg (see Fig. 1 for a site map). Except for oxygen, higher values on the y-axis represent higher stress levels. Dashed lines mark official German environmental quality targets (OGewV, 2016; red colour) or otherwise reported target values (Feld, 2013 for % crop in the catchment; UBA, 2003 for nitrate and potassium; black colour)

Notably, all six salt ions showed much higher mean concentrations at macrophyte-rich sites (significance not tested due to small sample size) (Table 2), hence confirming a pronounced tolerance of *S. pectinata*, which was the dominant species in the lower Wipper. The tolerance of *S. pectinata* towards salinisation was confirmed by data of 60 samples taken at 39 salinised river sites outside (but typologically comparable to) the Wipper system (Fig. 3). Apparently, the species can reach high a coverage (i.e., abundance class 4 or 5, translating to coverages of 25–50% or 50–100%, respectively, according to Kohler, 1978 and Londo, 1974) already at chloride levels around 250 mg/L. Furthermore, the species seems to respond fairly tolerant to enhanced concentrations of sulphate and potassium. It is important to note that both the findings in the Wipper system and at comparable sites outside the

system do not imply a boost of *S. pectinata* by salt, but confirm the pronounced tolerance of the species towards (chloride) salinisation.

High-resolution time-series monitoring revealed strong oxygen deficits at the macrophyte-rich site Hachelbich (Table 3), with 49% of nigh-time measurements not meeting the (German) quality target of 7 mg/L oxygen concentration. Contrastingly, high-resolution oxygen measurements at the macrophyte-poor site Bleicherode did not exhibit notable phases with oxygen depletion during night-time, and > 93% of all measurements (day + night) met the quality target 7 mg/L. Diurnal differences in high-resolution measurements of other physical and chemical variables were negligible, except for water temperature, which on average was 1 centigrade (= 1 Kelvin) lower during nighttime at all sites (Table 3).

Table 2 Overview of stressor levels at macrophyte-rich and macrophyte-poor sites in the Wipper system. Macrophyte-rich = coverage classes 4 (= > 25–50% coverage) and 5 (> 50–100%) according to Kohler (1978) and Londo (1974)

Parameter group	Parameter	Macrophyte-rich Mean ± SD	Macrophyte-poor Mean ± SD
Metadata	Period	2016	2016
	No. of sites	$N=3$	$N=4$
	General degradation macro-invertebrates (EQR)	0.35 ± 0.15	0.02 ± 0.03
Physical	O2 (mg/L)	6.7 ± 1,3	10.7 ± 0.9
	pH	8 ± 0,2	8.3 ± 0.1
	Electr. conductivity (µS/cm)	4947 ± 512	1222 ± 476
	T water (° C)	16.4 ± 0.9	10 ± 0.8
Nutrients	NH4-N (mg/L)	0.07 ± 0.09	0.02 ± 0.01
	NO3-N (mg/L)	2.29 ± 0.45	5.47 ± 0.24
	o-PO4-P (mg/L)	0.12 ± 0.02	0.06 ± 0.05
	Ptot (mg/L)	0.25 ± 0.03	0.11 ± 0.09
Salt	Cl (mg/L)	1340 ± 251	148 ± 131
	SO4 (mg/L)	388 ± 98	178 ± 63
	K (mg/L)	70 ± 11	10 ± 7
	Na (mg/L)	607 ± 124	67 ± 53
	Mg (mg/L)	105 ± 5	28 ± 9
	Ca (mg/L)	254 ± 19	158 ± 26
Physical habitat	Habitat index	5.3 ± 0.6	4.8 ± 1.7
Catchment land use	Crop land (%)	78 ± 30	69 ± 11
	Grassland (%)	5 ± 7	5 ± 4
	Urban (%)	2 ± 3	4 ± 2
	Forest (%)	15 ± 20	23 ± 12

Fig. 3 Coverage of *Stuckenia [Potamogeton] pectinata* against the concentration of chloride, sulphate, sodium and potassium in an external dataset of 60 samples from 39 river sites outside the Wipper system in Germany. External river sites were constrained to the same three river types that occurred in the Wipper system (6, 7 and 9.1 acc. to Pottgiesser, 2018). Coverage according to Londo (1974): 1 = < 1% coverage, 2 = 1–5%, 3 = > 5–25%, 4 = > 25–50%, 5 = > 50–100%
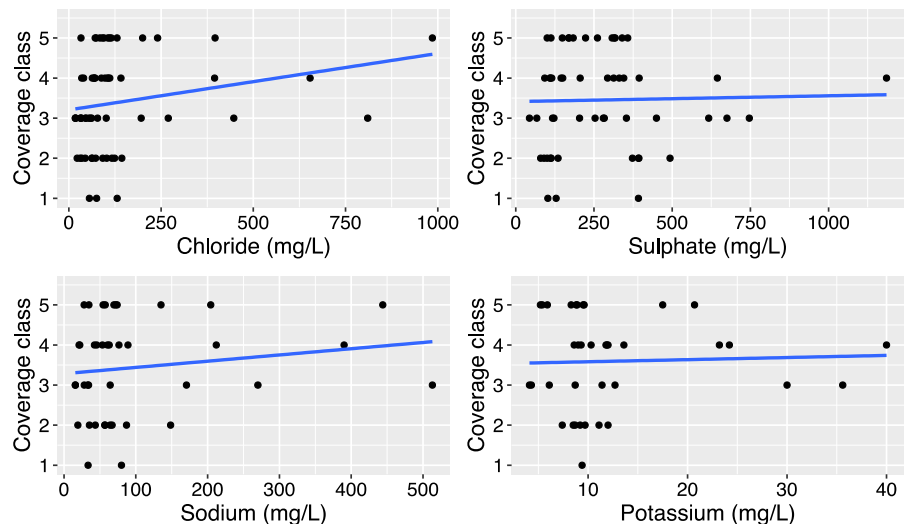
Table 3 Summary of high-resolution (15 min intervals) time-series data of physical and chemical stressors at two automatic probe locations (Bleicherode and Hachelbich) during the main vegetation period (April 1st–October 31st, 2016). Daytime was set to the estimated time of primary production, i. e. one hour after sunrise until sunset (sunrise/sunset corrected for daily changes)

Environmental variable	Probe	Statistical parameter	Bleicherode		Hachelbich	
			Day	Night	Day	Night
Electric conductivity (µS/cm)	TetraCon 700 IQ, Xylem Analytics (WTW), Weilheim, Germany	Median (Q25–Q75)	1141 (607–1267)	1132 (652–1220)	5377 (5057–5701)	5316 (5007–5621)
		Mean (SD)	958 (389)	958 (342)	5346 (462)	5273 (446)
K (mg/L)	TetraCon 700 IQ, Xylem Analytics (WTW), Weilheim, Germany	Median (Q25–Q75)	26 (16–34)	28 (16–35)	58 (51–64)	57 (51–65)
		Mean (SD)	25 (12)	26 (12)	58 (10)	58 (10)
NH_4 (mg/L)	Varion plus AN/A, Xylem Analytics (WTW), Weilheim, Germany	Median (Q25–Q75)	0.11 (0.1–0.19)	0.1 (0.1–0.17)	0.3 (0.13–0.48)	0.28 (0.15–0.44)
		Mean (SD)	0.15 (0.08)	0.14 (0.08)	0.35 (0.24)	0.33 (0.22)
NO_3 (mg/L)	Varion plus AN/A, Xylem Analytics (WTW), Weilheim, Germany	Median (Q25–Q75)	4.17 (3.29–5.03)	4.34 (3.53–5.26)	2 (1.13–2.68)	1.97 (1.03–2.64)
		Mean (SD)	4.04 (1.42)	4.24 (1.41)	1.89 (1.04)	1.83 (1.09)
O_2 (mg/L)	FDO 700 IQ, Xylem Analytics (WTW), Weilheim, Germany	Median (Q25–Q75)	9.5 (8.7–10.5)	8.6 (8–9.7)	10 (8.3–11.9)	7 (5.6–8.7)
		Mean (SD)	9.6 (1.7)	8.7 (1.1)	10.1 (2.8)	7.2 (2.1)
pH	SensoLyt 700 IQ/SEA, Xylem Analytics (WTW), Weilheim, Germany	Median (Q25–Q75)	8.2 (8.1–8.3)	8.1 (8–8.2)	8.4 (8.2–8.5)	8.3 (8.1–8.4)
		Mean (SD)	8.2 (0.2)	8.1 (0.1)	8.4 (0.2)	8.3 (0.2)
T_{water} (°C)	TetraCon 700 IQ, Xylem Analytics (WTW), Weilheim, Germany	Median (Q25–Q75)	15.1 (11.1–16.8)	14.1 (10.2–15.9)	17.6 (14.1–19.3)	16.8 (11.9–18.4)
		Mean (SD)	14.7 (4)	13.7 (4)	16.6 (3.8)	15.6 (3.8)

Effects of water and habitat quality on macroinvertebrates

Variance inflation factor analysis revealed five non-collinear stressors in the Wipper system ($N = 9$ sites) allocated to three stressor groups: (i) nutrients (ammonia, ortho-phosphate), (ii) salt (chloride, sulphate) and (iii) physical habitat (habitat quality index 'GSG'). Percent catchment land uses (crop land, urban area) of sites were invariable along the river continuum and thus excluded from the analysis. When subjected to a PCA, two main components showed eigenvalues above 1 and sufficed to explain 70% of the variability in the stressor data (Fig. 4). PCA 1 (49.4%) described a water quality gradient subsuming the impacts of enhanced nutrient and salt concentrations. PCA 2 (20.6%) described a gradient of physical habitat degradation. Because PCA components are mutually orthogonal (uncorrelated) variables, both main
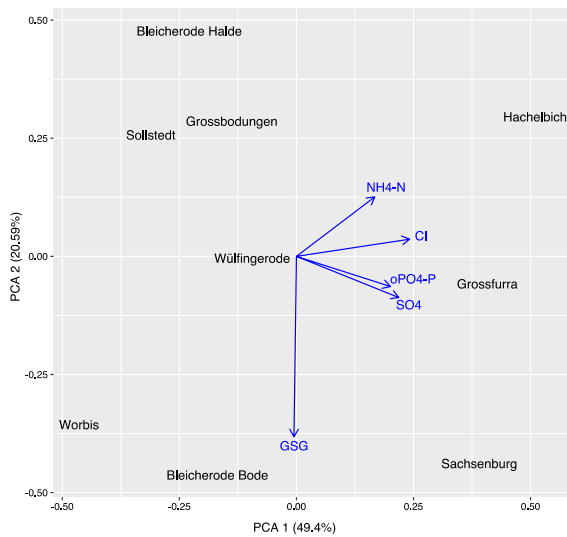
Fig. 4 Biplot of a PCA on values of five non-collinear stressor variables measured at nine sites in the Wipper system. Both main components PCA 1 and 2 have an eigenvalue above 1 and together explain 70% of the variability in the data. Stressor variables are ammonia–nitrogen (NH4-N), chloride (Cl), ortho-phosphate phosphorus (oPO4-P), sulphate (SO4) and physical habitat quality (GSG)

stressor gradients were considered independent of each other.

To contrast both stressor gradients with the organisms' response, the sample sites' PCA scores were extracted and correlated with two macroinvertebrate indices, namely the common degradation index (AD_EQR) and the proportion of EPT specimens (EPT_EQR) (Fig. 5). Correlations were notably stronger for the water quality component ($r = -0.78$, $P < 0.05$ and $r = -0.81$, $P < 0.01$, respectively) as compared to the physical habitat component ($r = 0.27$ and $r = 0.20$, respectively; both insignificant). The findings confirm water quality issues to be the major descriptor of macroinvertebrate ecological deterioration in river Wipper. However, although much smaller and insignificant, the trends of both biological metrics along the (uncorrelated) second PCA component suggest an indicative potential of macroinvertebrates for physical habitat degradation even under the pronounced influence of salinisation. The trend becomes particularly obvious for the common degradation index (AD_EQR) with samples of moderate to poor status (Fig. 5, yellow and orange dots in plot on the top righ-hand side).

Discussion

River management requires management solutions that are tailored to the individual pressures and impacts of the water bodies of interest. This is one of the main conclusions of a recent pan-European project summarising nearly 70 studies on biological effects of a total of 174 stressor pairs in freshwater and marine ecosystems (Birk et al., 2020). Rivers across Europe turned out to be frequently impacted by a concert of impacts by, for example, nutrients, pesticides, oxygen depletion, warming, hydrological alteration, physical habitat degradation and land use, which eventually seem to drive complex biological responses.

Biological responses to water and habitat quality deterioration in the Wipper

Our study supports the conclusion by Birk et al. (2020) also for the Wipper system. The entire river course, including its major tributary, was affected by the influence of multiple chemical compounds originating from diffuse and point sources of pollution as well as from hydromorphological alterations of the river course. Yet, in addition the obvious mass development of salt-tolerant aquatic macrophytes, namely of *S. pectinata*, adds complexity to the environmental and biological deterioration of river Wipper, in that the plant species seems to link between direct (i.e., osmotic) and indirect (i.e., respiratory) adverse effects of salinisation on the macroinvertebrate community.

The most obvious direct effect is probably caused by a mixture of salt ions originating from the controlled and diffuse discharge of brine. Chloride levels, for example, quickly rose already in the upper part of the river and exceeded 1 g/L in the lower part. In light of current environmental quality targets in Germany (OGewV, 2016) and further proposed quality targets (Sundermann et al., 2015; Halle et al., 2017), strong adverse effects of chloride levels way beyond 1 g/L are very likely. Chloride, as many other salt ions, is known to impose direct and strong physiological stress on the aquatic stages of macroinvertebrates in that it enhances the water's osmolarity. Because many macroinvertebrates possess only weak osmoregulatory capabilities (Wolfram et al., 2014), an increase of the osmolarity in the ambient medium is usually followed by a rapid increase of the osmolarity in the cell
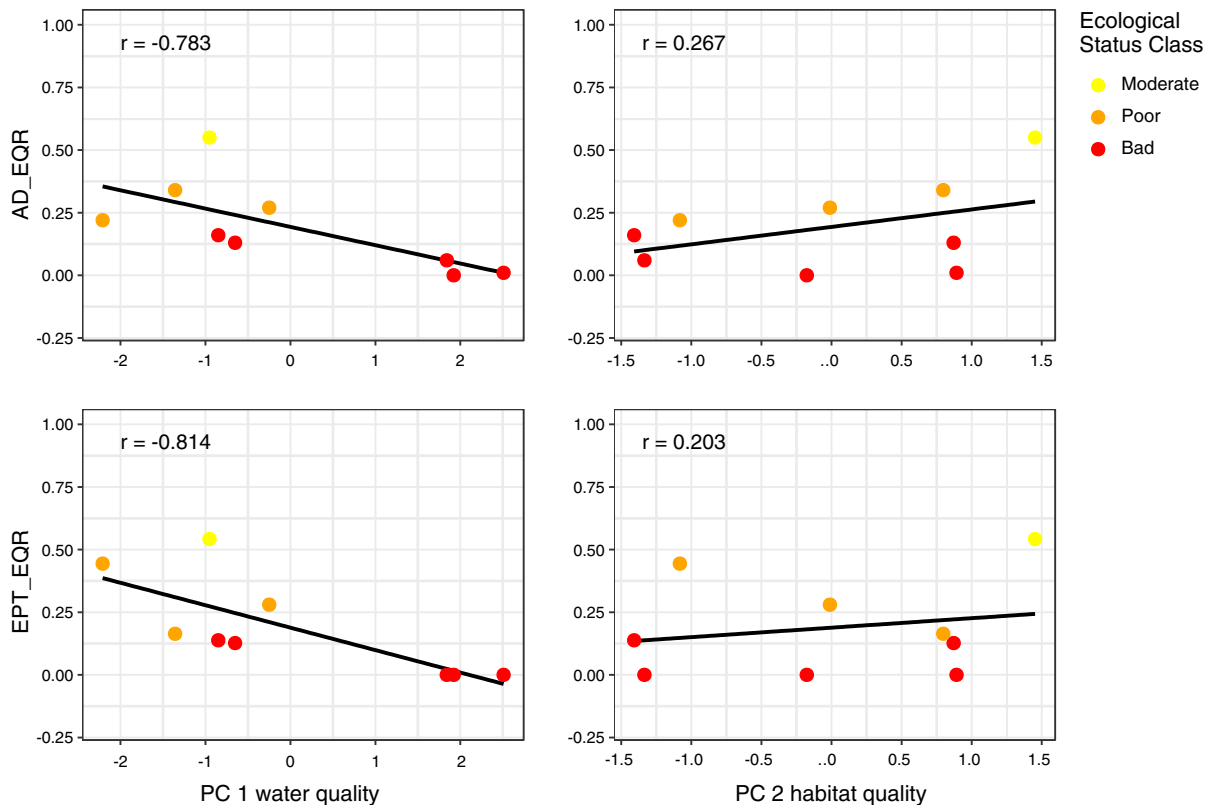
Fig. 5 Relationship of a macroinvertebrate common degradation index (AD_EQR) and the proportion of EPT (Ephemeroptera, Plecoptera, Trichoptera) specimens (EPT_EQR) with the two main principal components PC 1 (water quality) and PC 2 (habitat quality) as derived from the PCA (compare Fig. 4). Note that positive PC scores correspond to low water qual-ity and high habitat quality, respectively. Spearman's correlation coefficients are indicated in the top left of each plot. EQR stands for ecological quality ratio and ranges from 0 (poor quality) to 1 (high quality). The dots (sites) are colour coded according to their overall ecological classification

medium, which is lethal for many freshwater species. The toxicity of single ions (e. g., chloride, potassium) to freshwater macroinvertebrates has been described in detail by Schulz & Cañedo-Argüelles (2018).

Besides salinisation, our results revealed also enhanced nutrient levels, namely of phosphate and nitrate, to affect the water quality in the Wipper. Yet, in light of the observed concentrations of both compounds, direct physiological effects on benthic invertebrates seem rather unlikely (see Wang et al., 2013 for a discussion of direct *vs.* indirect nutrient effects). More likely, enhanced phosphorus and nitrogen levels may have driven primary production (Ouyang et al., 2018) and hence the mass development of aquatic macrophytes and algae in the lower Wipper. In this context, the decrease in the concentration of nitrate nitrogen in the lower Wipper may seem contradictory

at first glance, yet may be explained by the plant's uptake (retention) of nitrogen. In contrast, the increase of ortho-phosphate phosphorus in the lower Wipper suggests a continuous supply, for example, by point source pollution, which may have masked its retention in the plant biomass.

The direct influence of hydromorphological alterations of the Wipper on macroinvertebrates was less pronounced. Two macroinvertebrate community metrics revealed weak and insignificant correlations with a hydromorphological gradient, yet nevertheless suggest that structural deficiencies (e.g., lack of natural microhabitats, bank enforcement, lack of natural riparian vegetation) along the river course remain detectable by macroinvertebrates even under the influence of salinisation. At least for one metric (AD_EQR), a stronger trend would be observable with sites

of moderate and poor ecological status (Fig. 5, plot of AD_EQR along PCA 2). The "bad" sites, however, may already have undergone a dramatic loss of species so that the remaining species pool was insufficient to track changes in the habitat quality. However, in light of the small sample size available for river Wipper, this assumption remains speculative and requires further evidence.

Macrophytes as connectors between osmoregulatory and respiratory stress on benthic macroinvertebrates

The strong positive relationship between salinisation and the mass development of macrophytes, namely of *S. pectinata* in the Wipper was striking and was supported by the analysis of data from similar rivers outside the Wipper system. Furthermore, because salt (Cl and K) was stronger correlated to macrophyte coverage than habitat quality (overall and bank quality) in the Wipper, it seems likely that salinity favoured the mass development of *S. pectinata*. There is sufficient evidence that salt-tolerant macrophytes (alike *S. pectinata*) can develop a high abundance even under heavily salinised conditions, with chloride concentrations beyond 1.4 g/L. While the tolerance of *S. pectinata* towards salinisation has been reported also by other studies (Wolfram et al., 2014), detailed studies on the physiological mechanisms controlling the salt tolerance of aquatic plants are sparse (e. g. by Simmons (2012) on the duckweed *L. minor* L. or by Rout & Shaw (2001) on some naiads *Najas* sp.). The studies suggest that the plant's tolerance against chloride or sulphate may be controlled by potassium and other cations. Potassium-mediated stress tolerance is well reported for terrestrial plants, namely for crops such as barley (Wang et al., 2013), where potassium not only can help increase the plants tolerance against salinisation, but also its tolerance against other stressor, for example, drought stress. This explains, why potassium (as potash/potassium chloride, KCl) is supplied to agricultural crops. The high concentrations of potassium and chloride in river Wipper are directly linked to potash mining that took place mainly between the1890s and 1990s in the upper catchment. Nowadays, brine drainage from several open salt dumps in the catchment constantly convey salt into the Wipper—and will probably continue to do so for the next couple of decades (estimation

by co-author CJS, State Office for the Environment, Mining and Nature Protection Thuringia).

The automatic probe measurements of oxygen levels at two sites in the Wipper revealed notable oxygen deficiencies at the macrophyte-rich site at Hachelbich during nighttime, as opposed to the macrophyte-poor site at Bleicherode. At Hachelbich, nocturnal oxygen concentrations frequently dropped below the German target level required to maintain a good ecological status (i.e., 7 mg/L; OGewV, 2016), while daytime oxygen levels at the same station ranged around 10 mg/L. This strong diurnal fluctuation of oxygen levels at Hachelbich can be explained by diurnal physiological patterns of primary producers. During daytime, photosynthesis is driven by sunlight and oxygen is produced. During nighttime, photosynthesis is replaced by mitochondrial respiration and the plants consume more oxygen than they produce. Oxygen consumption also appears during the aerobic degradation of plant biomass by microorganisms at the end of the vegetation period. Such plant-driven oxygen deficits, however, are likely to be overlooked by standard monitoring schemes, which usually involve oxygen measurements during daytime.

The frequent drops of oxygen levels below 6 mg/L that were observed for nearly 50% of the nighttime measurements at Hachelbich probably also occurred at other macrophyte-dominated sites in the lower Wipper. Hence, oxygen supply in the lower river was probably unfavourable for many macroinvertebrate species at nighttime during the summer period. Similar to salinisation, oxygen depletion has a direct physiological effect on the aquatic life stages of macroinvertebrates. Thereby, species without particular respiratory structures (e.g., gills) such as many plecopteran larvae respond more sensitive as opposed to ephemeropterans and trichopterans, whose larvae possess gills.

Implications for river management under the influence of salinisation

Due to its direct, osmo-regulatory effects on the physiology of both plants and animals salinisation constitutes a severe stressor of aquatic ecosystems (Beisel et al., 2011; Wolfram et al., 2014), whereas its effects might be boosted by climate change (Melles et al., 2023). Thereby, salt ions are not degradable and may accumulate in groundwater aquifers, sediments and

biomass. This persistence of salt in ecosystems constitutes a long-term threat, which is likely to increase rapidly under the influence of global warming (Jeppesen et al., 2020), in particular in semiarid, but nevertheless agriculturally used regions around the world, such as the south-western USA, Mediterranean Europe, southern Africa, east Asia and Australia.

In concert, our findings suggest that a stressor (here: salt) can favour a biological response (here: boost of *S. pectinata* under salinisation) that in itself constitutes another stressor (here: oxygen depletion) with adverse effects on another organism group (here: macroinvertebrates). This complex interaction of osmoregulatory and respiratory stressors, which is caused by primary production, requires consideration in the management of salinised rivers.

Conclusion

Salinisation has direct and detrimental physiological effects on freshwater organisms. However, salinisation may favour particularly tolerant macrophyte species and then promote their mass development, which in turn may result in oxygen depletion in dense macrophyte stands during nighttime. Salt-tolerant species such as *S. pectinata* outcompete salt-sensitive species and can reach very high a coverage on the river bottom. Besides oxygen depletion during nighttime, the recent fish-kill in river Odra and the subsequent investigation of potential causes support such plant-driven effects of salinisation on other water quality parameters. In case of the recent fish-kill in river Odra, it was salinisation too that was assumed to have boosted the mass development of an golden algae (*Prymnesium parvum* N.Carter), whose toxicants are lethal for fish (IGB, 2022).

River management should acknowledge both the interaction of stressors and the role of biological responses as linkage between stressors. This includes the use of automatic probes, for example, to identify diurnal rhythms of particular stressors such as oxygen depletion, which tend to remain undetected by monitoring schemes applying daytime spot measures. In the long-term, however, a significant reduction of salt loads would be required to reduce the risk of unforeseen side effects and ultimately to achieve an ecological improvement of the aquatic communities.

Data availability All data analysed for this article were obtained through national monitoring schemes in line with the demands of the European Water Framework Directive. Monitoring data are available on request at the Thüringer Landesamt für Umwelt, Bergbau und Naturschutz (TLUBN), Göschwitzer Str. 41, 07,745 Jena, Germany.

Declarations

Conflict of interest All authors declare that they have no competing interests in any material discussed in this article.

Ethical approval The authors have no ethical conflict to state.

Consent to participate The research leading to the results presented in this article did not involve animal experiments or humans.

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