Relating environmental pressures to littoral biological water quality indicators in Western Balkan lakes: Can we fill the largest gaps?

Jan E. Vermaat [a],*, Vera Biberdžić [b], Vjola Braho [c], Biljana Budzakoska Gjoreska [d], Magdalena Cara [c], Zamira Dana [c], Pavle Đurašković [e], Tor Erik Eriksen [m], Dag Hjermann [m], Alma Imeri [c], Katarina Jovanović [f], Jelena Krizmanić [g], Lirika Kupe [c], Tatjana Loshkoska [h], Joanna Lynn Kemp [m], Aleksandra Marković [i], Suzana Patceva [d], Jelena Rakočević [j], Katarina Stojanović [k], Marina Talevska [d], Sonja Trajanovska [d], Sasho Trajanovski [d], Elizabeta Veljanoska-Sarafiloska [d], Danijela Vidaković [i], Konstantin Zdraveski [l], Ivana Živić [k], Susanne C. Schneider [m]

[a] Faculty of Environmental Sciences and Nature Conservation, Norwegian University of Life Sciences, P.O.Box 5003, 1430 Ås, Norway
[b] Natural History Museum of Montenegro, Bećir bega Osmanagića 16, 81000 Podgorica, Montenegro
[c] Agricultural University of Tirana, Faculty of Agriculture and Environment, Paisi Vodica, Kodër-Kamza, Tirana, Albania
[d] Hydrobiological Institute Ohrid, Naum Ohridski 50, 6000 Ohrid, Macedonia
[e] Institute of Hydrometeorology and Seismology, 4th Proleterske brigade 19, 81000 Podgorica, Montenegro
[f] Institute of Public Health of Serbia Dr Milan Jovanović Batut, dr Subotića starijeg 5, 11000 Belgrade, Serbia
[g] University of Belgrade, Faculty of Biology, Institute of Botany and Botanical Garden "Jevremovac", 43 Takovska, Belgrade 11000, Serbia
[h] Primary School Kocho Racin, "130", 24, Ohrid 6000, Macedonia
[i] University of Belgrade, Institute of Chemistry, Technology and Metallurgy, National Institute of the Republic of Serbia, Njegoševa 12, Belgrade 11000, Serbia
[j] University of Montenegro, Faculty of Natural Sciences and Mathematics, Biology Department, 81000 Podgorica, Montenegro
[k] University of Belgrade, Faculty of Biology, Studentski trg 16, 11 000 Belgrade, Serbia
[l] Public Institution Galicica National Park, Department of Alternative Activities and Environmental Education, Velestovski pat b.b., 6000 Ohrid, Macedonia
[m] Norwegian Institute for Water Research, Gaustadalleen 21, 0349 Oslo, Norway

HIGHLIGHTS

- We assessed three pressures on littoral biological indicators in 6 Balkan lakes.
- Six littoral transects in each lake varied in water quality and surrounding land use.
- Abundance and diversity of macrophytes, diatoms and invertebrates were used.
- Most important pressures were water level fluctuation and eutrophication due to urbanization.
- Shoreline alteration was less important in explaining indicator variability.

GRAPHICAL ABSTRACT
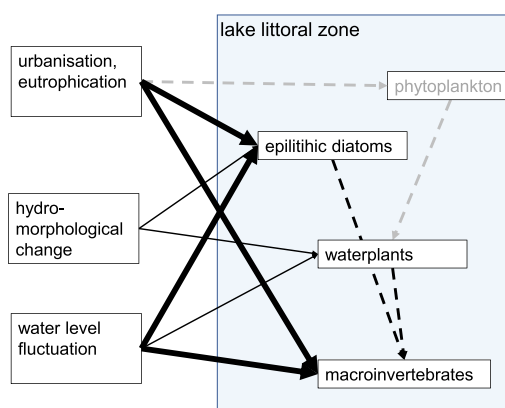
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* Corresponding author.
    E-mail address: jan.vermaat@nmbu.no (J.E. Vermaat).

ABSTRACT

Along six transects in each of six lakes across the Western Balkans, we collected data for three groups of littoral biological water quality indicators: epilithic diatoms, macrophytes, and benthic invertebrates. We assessed the relationships between them and three environmental pressures: nutrient load (eutrophication), hydro-morphological alteration of the shoreline, and water level variation, separating the effect of individual lakes

and continuous explanatory variables. Lake water total phosphorus concentration (TP) showed substantial variation but was not related to any of the tested biological indicators, nor to any of the tested pressures. We suggest that this may be due to feedback processes such as P removal in the lake littoral zone. Instead, we found that a gradient in surrounding land-use towards increasing urbanization, and a land-use-based estimate of P run-off, served as a better descriptor of eutrophication. Overall, eutrophication and water level fluctuation were most important for explaining variation in the assessed indicators, whereas shoreline hydro-morphological alteration was less important. Diatom indicators were most responsive to all three pressures, whereas macrophyte biomass and species number responded only to water level fluctuation. The Trophic Diatom Index for Lakes (TDIL) was negatively related to urbanization and wave exposure. This indicates that it is a suitable indicator for pressures related to urbanization, although a confounding effect of wave exposure is possible. Invertebrate abundance responded strongly to eutrophication, but the indicator based on taxonomic composition (Average Score Per Taxon) did not. Our results suggest that our metrics can be applied in Western Balkan lakes, despite the high number of endemic species present in some of these lakes. We argue that local water management should focus on abating the causes of eutrophication and water level fluctuation, whilst preserving sufficient lengths of undeveloped shoreline to ensure good water quality in the long run.

1. Introduction

The implementation of the Water Framework Directive across the European Union is a major effort to harmonize and improve water quality assessment (a.o. Birk et al., 2012, Poikane et al., 2014). Poikane et al. (2015) reported that both data and methodological harmonization efforts from eastern continental Europe and the Mediterranean are few, and that, in particular, overall assessments of combined pressures are lacking. Poikane et al. (2015) suggested that for the Mediterranean this may be partly related to the small absolute number of lakes present, their unique character and often small size. Since then, also for these areas assessment methods have been developed and intercalibrated (e.g. Ntislidou et al., 2018; Zervas et al., 2018), but gaps remain. Our consortium collected a multi-indicator data set from the littoral zones of six lakes in the Western Balkans, a region adjacent to the Mediterranean and eastern continental Europe. We used methods that are broadly consistent with the methodological requirements for these specific indicators as set out in the European Water Framework Directive (Schneider et al., 2020a). Our aim was to address the information gap for the Western Balkans and determine whether generalized conclusions can be drawn, or if each lake needs to be considered as a unique feature in the landscape.

We started from the DPSIR framework (**D**rivers – **P**ressures - **S**tate Change - (societal) **I**mpact - (policy) **R**esponse, e.g. Cooper, 2013) to structure our thinking about potentially interacting pressures that affect the different biological aspects of the lake ecosystem. We identified a priori the following three pressures as being potentially important (Poikane et al., 2014; Pilotto et al., 2015) and often independent (Johnson et al., 2018), being caused by different underlying societal drivers: increased nutrient-load leading to eutrophication, hydro-morphological change in the littoral zone due the construction of hard or sandy shores, and hydrological changes leading to altered seasonal water level fluctuation and wave erosion regimes. The latter two pressures have a direct impact on littoral communities, hence our focus on the littoral zone. The effects of these pressures on the ecosystem can sometimes be similar or even synergistic (e.g. both eutrophication and hard surfaces can increase the biomass of filamentous algae), but in other circumstances two effects may work against each other (e.g. eutrophication can increase plant biomass, while water level variation can decrease it). Together, these changes may have different ultimate consequences for societal use (summarized in Fig. 1). The six lakes - Sava, Prespa, Ohrid, Crno, Biogradsko and Lura - were selected to reflect a gradient in anthropogenic pressures based on variation in the proportion of agricultural and urban land cover in their surrounding area (cf Table 1 in Schneider et al., 2020a). Indeed, Schneider et al. (2020a) observed a threefold range in the mean concentration of total phosporus

(P) and an eightfold range in estimated external P-load, but did not examine other pressures.

Here we chose three littoral indicator groups (epilithic diatoms, macrophytes, and benthic invertebrates) which are part of the mandatory quality elements in the Water Framework Directive supported by a substantial literature (e.g. Birk et al., 2012; Poikane et al., 2015). Our consortium had the methodological competence to perform comparable analyses across four different countries in the Western Balkans.

Against the background of a naturally variable littoral geomorphology and nearshore land cover, we expected that, together, the three pressures would affect species assemblages and lead to a reduced diversity in all three biological indicator groups. The magnitude of the impact of each pressure and their interactive effects (e.g. Pilotto et al., 2015) were difficult to predict more specifically, however, because individual pressure-species richness relations are not necessarily linear (e.g. Astorga et al., 2011). We therefore asked the following exploratory questions:

(1) How much of the observed variance in diatom, macrophyte and macroinvertebrate indicators is explained by the different pressures? Which is more important, eutrophication, hydro-morphological change, or water level fluctuation?
(2) How strong is the covariance among the three indicator groups? Do they show the same patterns, or do they respond differently to the different pressures?
(3) How important is the unique character of the individual lakes relative to the effect of the three pressures?
(4) Can we draw any general conclusions for lake management in the Western Balkans?

2. Materials and methods

2.1. Studied lakes

We selected six lakes ranging greatly in size, geological origin and history, and adjacent human land use. The lakes Ohrid (693 m asl) and Prespa (849 m asl) are both large, comparatively old and have a complex geological origin. Both are fairly well studied (e.g. Stankovic, 1960; Spirkovski et al., 2001; Matzinger et al., 2006; Popovska and Bonacci, 2007; Schneider et al., 2014; Vermaat et al., 2020). Lake Sava (73 m asl) is a former arm of the river Sava within the city of Belgrade and intensively used for recreation (Jovanovic et al., 2017). The remaining three are comparatively small mountain lakes. The lakes Lura (1722 m asl) and Crno (1419 m asl) are likely to be cirques from the last glaciation (Radulevic et al. 2010, Vidakovic et al., 2020) and
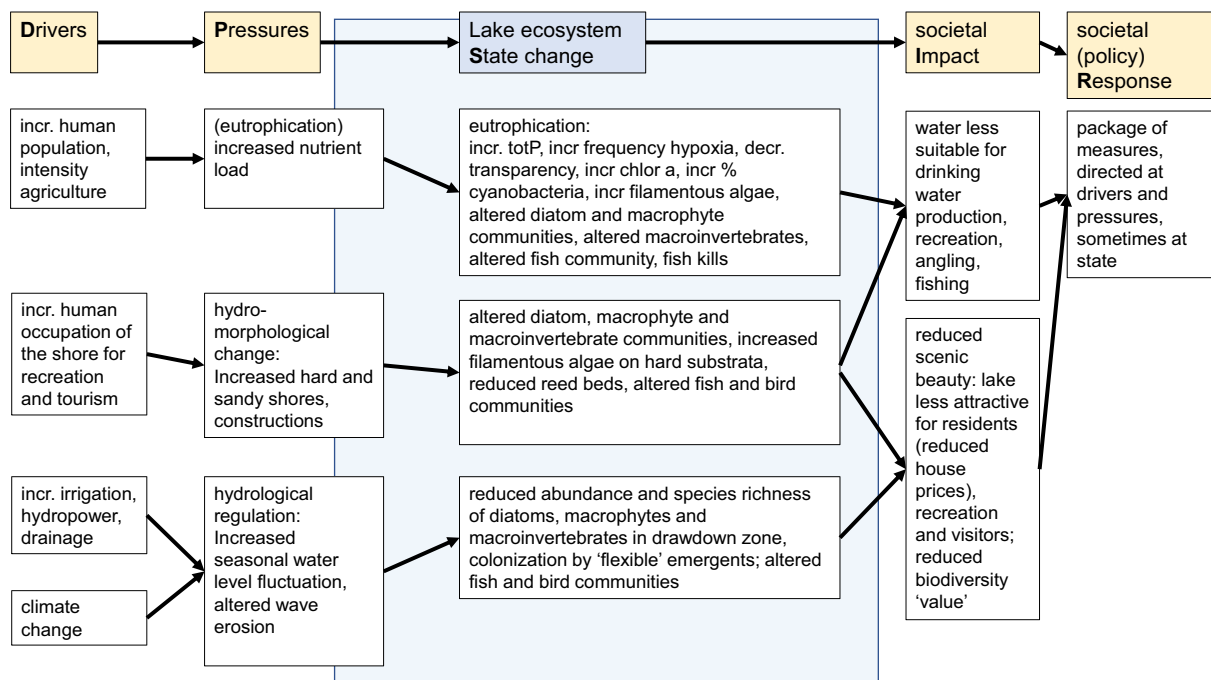
Fig. 1. Generalized a priori DPSIR framework combining three environmental pressures on Western Balkan lakes. A policy response can feed back to any of the other four elements.

Biogradsko (1094 m asl) is thought to be an infilling depression behind a moraine (Government of the Republic Montenegro, 1997). All three are in areas with a nature protection designation, although that does not mean there is no human activity. For example, Vidakovic et al. (2020) documented large-scale deforestation of the slopes surrounding Lake Lura. The Crno and Biogradsko Lakes receive large numbers of tourist visitors, as we personally witnessed during our field work.

2.2. Variables included

The field collection campaigns in 2016, 2017 and 2018 and the subsequent processing and analysis of the data followed standard protocols. This has been described exhaustively in Schneider et al. (2020a). A brief summary of the methods is given in Table S1. Variables included in this study are briefly described in Table 1. We included water total P, sediment total P and sediment organic matter from the original set of variables in Schneider et al. (2020a), because total P is commonly viewed as reflecting eutrophication, and sediment may be used as a source of P by aquatic macrophytes. Habitat characteristics of the littoral zone were also quantified. These were: the presence of gravel beaches; shoreline modification for anthropogenic use; presence of emergent reed (*Phragmites australis*) stands in the foreshore; fetch (as a measure of wave exposure); and an index of annual water level fluctuation (Table 1, see also below). Sediment organic matter may also respond to changes in water level, and to increased hard shorelines (harnessing) as these lead to increased wave turbulence.

We estimated the extent of seasonal water level fluctuation from literature (Popovska and Bonacci, 2007; Radulovic et al., 2010; Vidakovic et al., 2020) and our own field experience. A simple indicator of fetch, or wave exposure, of a littoral station to wind-induced wave action was estimated from the length of a perpendicular line from the shore towards the opposite shore. This is equivalent to the 'maximum fetch' of Rowan et al. (1992). We refrained from more elaborate indices because we only needed a comparative indicator for our six lakes of very different sizes. Rowan et al. (1992) suggested that the maximum fetch had very similar explanatory power in predicting mud deposition depth when compared to a more elaborate indicator of exposure (both equations include littoral slope, 89

vs 93% explained variance). We abstained from a further condensation of these environmental variables into one compound, common indicator, such as the Lake Habitat Modification Score (e.g. McGoff et al., 2013a; Pilotto et al., 2015), since we were interested in the possible effects of the individual components.

We included the following macrophyte variables for the following reasons: species richness, because large seasonal fluctuations in water level compresses the habitat available for submerged macrophytes and hence the likely number of species (e.g. Rørslett, 1984); the lower vegetation limit, as it responds to eutrophication-related increases in turbidity (e.g. Middelboe and Markager, 1997); abundance estimates for *Cladophora*, because this may increase with eutrophication (Depew et al., 2011)); the abundance of charophytes, because this generally declines with eutrophication (Blindow, 1992); and the overall biomass of macrophytes, because this has been shown to increase with P runoff from the adjacent land; Schneider et al., 2020a). We also looked at a transition in species composition with increasing nutrient load (cf. Poikane et al., 2018; Hilt et al., 2018) and at growth form spectra (Radomski and Goeman, 2001) but experienced limited resolution for lakes with few species, so we do not report on the latter. Similarly, we could not include a composite macrophyte index, such as the Balkan Macrophyte Index BMI (Schneider et al., 2020b), because a reliable calculation of the index was not possible in three of our six lakes due to a limited number of species and/or abundances.

For diatoms we included an overall taxon richness index, because increases in macrophyte diversity are likely to increase the richness in habitats available for diatoms (Blindow, 1987) and this may also affect epilithic species richness indirectly. Shoreline harnessing, however, may mainly favor prostate epilithic taxa that can cope with heavier wave turbulence caused by reflection, and thus reduce species richness. Increased water level fluctuation may reduce the time window for colonization and thus favor small, rapidly dispersing and fast-growing diatom taxa, hence reducing species richness. We also included the Trophic Diatom Index for Lakes (TDIL; Stenger-Kovács et al., 2007), as it is designed to indicate eutrophication and has been specifically developed for lakes. TDIL was chosen from several alternative composite diatom indicators as it correlated most closely to nutrient run-off in Schneider et al. (2020a).

Table 1
Variables included in this study. Total number of observations is 36 with 6 stations sampled at 6 lakes, unless otherwise stated. Medians (where relevant), means (where greatly different from medians) and ranges are reported.

Variable name	Description	Median (mean), range, units
pc1_urbanization	Principal component summarizing a gradient from rural to urban in land cover pooled from the three land cover zones (0-20 m, 20–100 m, 500 m trapezoids), see methods for further explanation	−1.1–2.5, scaled, unitless
pc2_deciduous to coniferous	Principal component summarizing a gradient from deciduous to coniferous woodland, marshes in the 0-20 m band covaried strongly.	−1.9–2.5, scaled, unitless
P run-off	Estimate combined from CORINE land use in the 500 m trapezoids and export coefficients from Smith et al. (2005), expressed per unit area land.	0.4; 0.2–4.8 kg P ha^{-1} y^{-1}
Shoreline harnessing[a]	Hard hydromorphological alteration. Assessed in the field, percentage cover of the shore by all concrete, riprap, stones and other artificial embankment structures; Table S3.	0 (mean 0.6); 0–4
Gravel beach[a]	As shoreline harnessing	0.5 (mean 1.8); 0–4
Water reed before the shore[a]	As shoreline harnessing	0 (mean 0.6); 0–4
Fetch	Length of a perpendicular line to the opposite shore (see methods), indicator of wind-induced wave exposure	0.5 (mean 4.1); 0.1–29.4 km
Seasonal water level fluctuation	Estimated annual range (see methods)	1; 0.5–3 m
Water total P	Total P content of unfiltered littoral water sample taken at 0.5 m depth; mean of spring and autumn sampling; means from spring and autumn sampling are used.	13; 4.9–29.1 µg L^{-1}
Sediment organic matter	Sediment organic matter from a sediment grab sample taken at 1 m depth, measured from weight loss on ignition; means from spring and autumn sampling are used.	3.6; 1.2–28.6%
Sediment total P	Sediment total P content taken from the same grab; means from spring and autumn sampling are used.	396; 134–3210 mg kg^{-1}
Macrophyte mass	Estimated a s the summed cube of all macrophyte abundance estimates in the transect down to 2 m (see Schneider et al., 2020)	103; 0–786
Cladophora mass	Same for Cladophora	0 (mean 50); 0–383
Sum Chara	Summed abundance of all Chara taxa in the transect down to 2 m; five point scale: 1 = very rare, 2 = infrequent, 3 = common, 4 = frequent, 5 = abundant, predominant	0 (mean 0.7); 0–4.5
Macrophyte species richness	Total number of species encountered at a transect down to 2 m.	3; 0–13
Lower vegetation limit	Lower vegetation limit at each transect assessed by snorkeling or grab sampling at greater depths	4; 0–16 m
Diatom number of species	See method in Schneider et al. (2020)	68; 23–102 per 5 stones
Diatom TDIL index	Index based on diatom species niche characteristics in calculated from the OMNIDIA data base, see Schneider et al. (2020). Low values indicate nutrient enriched.	14; 9.0–15.3
Invertebrate abundance at 2 m depth	Total number of individuals estimated from subsampling (n = 33); means from spring and autumn and 2 m depth are used.	425; 0–2950 ind. m^{-2}
Invertebrate taxon richness at 2 m depth	Taxon richness, oligochaeta and chironomidae to family level, others to species (n = 33); spring values from 2 m depth are used.	5; 0–19
Invertebrate ASPT index	Average Score Per Taxon, indicator of organic pollution estimated with the ASTERICS tool, see Schneider et al. (2020, n = 27); low values indicate high organic loading; spring values from 2 m depth are used.	3.0; 1.5–8.5

[a] These variables were scored on the protocol in Supplementary table S3. All use a five point scale: 0, 1 ≤ 25%, 2 ≤ 50%, 3 ≤ 75%, 4 ≥75–100%.

For benthic invertebrates we selected overall abundance, because eutrophication may lead to increases in overall invertebrate abundance due to increases in certain groups (e.g. Sandin and Johnson, 2000). We also selected taxon richness because macrophyte-rich littoral zones with bands of emergent plants and trees along the shore were shown to be particularly species rich (Jurca et al., 2012), while wave-exposed gravel or hard substrates have less species rich but specialized assemblages (Brauns et al., 2011). Also, anthropogenic shoreline alteration reportedly leads to reduced macroinvertebrate richness (Brauns et al., 2007; McGoff et al., 2013b; Miler et al., 2015) as does increased water level fluctuation (Palomäki, 1994). In addition, we selected the Average Score Per Taxon index (ASPT), as a measure of changes to macroinvertebrate assemblages, because eutrophication may lead to shifts in invertebrate species composition through increased productivity (Johnson et al., 2018) and changes to macrophyte communities (Rasmussen, 1988), possibly in a non-linear manner, depending on the severity of the nutrient loading gradient (Jurca et al., 2012). The ASPT was originally designed to indicate organic pollution in running waters (Armitage et al., 1983) but has also been used in lakes (Poikane et al., 2015) and as an effective indicator of eutrophication (Sandin and Johnson, 2000). We also chose it because its taxonomic level (family) allows cross-country comparisons. Indicator scores were estimated from existing databases: OMNIDIA (https://omnidia.fr) for diatoms and ASTERICS (https://www.gewaesser-bewertung-berechnung.de/index.php/home.html) for invertebrates as in e.g. Miler et al. (2013).

Land use was quantified in two ways. Firstly, in the field we visually estimated cover of CORINE land use classes (EEA (European Environment Agency), 2014), both in the immediate nearshore littoral fringe (0–20 m inland) and in the adjacent band from 20 to 100 m for each station using a standard protocol (supplementary material Table S3). In addition, we quantified the presence of water reed (i.e. *Phragmites australis* rooting under water), rocks, gravel or sandy beaches, concrete walls and pipe outlets on the shoreline. Secondly, the wider near-shore land use was quantified from the latest CORINE land use map for a trapezoid of 10 ha area that stretched 500 m inland from the shore of the lake, with a width of 100 m at the shore and 300 m at the other end. Phosphorus run-off from the adjacent land in these trapezoids was estimated by summing the multiplier of the CORINE land use class area with specific export coefficients from Smith et al. (2005). The substantial covariance of land use across the 0–20 m and 20–100 m bands as well as the 500 m trapezoids has been accommodated by data reduction with principal component analysis (PCA). We included all individual cover variables from the three zones in one common PCA.

2.3. Data analysis

Data were analyzed with univariate GLM in SPSS version 26 with the different biological indicators as dependent variables, land use, lake morphology and chemistry as explanatory covariates and lake as a random factor, ensuring simultaneous assessment of both lake-specificity and general explanatory variables. For each indicator group, we included all covariates in the GLM model that could possibly be of meaningful influence. Hence, the GLM for water total P, for example, included

only the two land use principal components, P run-off and the shoreline indicators, whereas for invertebrates we also included fetch, water total P, sediment organic matter, sediment P, and macrophyte mass. GLMs were run with type III sums of squares, whereas relative contribution to explained variance was subsequently estimated with additive type I sums of squares. For error equality Levene's test was used, and we found $p > 0.02$ for all GLM runs done, so we decided that no transformations were necessary. We also ran multiple regressions with the same independent variables, but without the random factor 'lake', so that we could include water level fluctuation as an explanatory factor, a variable without within-lake replication. A comparison of the explained variance of the full GLM model and the multiple regression gives an indication of the strength of the factor 'lake', and of the continuous explanatory variables that may contribute to a between-lake effect.

3. Results

Pressure-gradients across the six lakes were considerable (Table 1). Together, exported P-load from the adjacent land (0.2–5 kg P ha^{-1} y^{-1}), water total P (5–30 µg P L^{-1}) and sediment total P (0.1–3.2 g kg^{-1}) reflected a substantial part of the ranges reported in the literature: exported P-load 0.2–4.9 kg P ha^{-1} y^{-1} (Smith et al., 2005); water total P concentration 7–690 µg P L^{-1}, median 34 µg P L^{-1} (European overview in Poikane et al., 2014, similar range in Donohue et al., 2009); Sediment total P 0.3–1.5 g kg^{-1} (Randall et al., 2019). Also, water level fluctuation (Fig. S1) and shoreline harnessing varied substantially across sites (Table 1).

Land-cover showed a similar pattern in the inner and outer littoral bands as in the larger trapezoids taken from CORINE. These patterns could be condensed into two synthetic principal components (Fig. 2): one reflecting a rural-urban gradient (more built-up area, roads, parks), and the other corresponding to a transition from deciduous to coniferous forests with a parallel increase in marshland in the inner 0–20 m band. The stations of the three mountain lakes form individual clusters that are spread along the second axis, whereas the stations in lakes Ohrid, Prespa and Sava vary most strongly along the first axis, but also along the second (Fig. 2 right). Interestingly, gravel beaches co-vary strongly and negatively with increased urbanization (Fig. 2, left).

Variation in water and sediment total P was explained best by the factor lake (Table 2, Table S2), rather than by P-load, or urbanization. The latter two co-varied significantly ($r^2 = 0.45$, $p < 0.001$, not shown). Lake Prespa had the highest water total P, whereas Biogradsko and Crno were highest in sediment P. Additional significant covariance with water total P was found with water level fluctuation, the presence of inshore reed beds and gravel shores. In the multiple regression without the factor lake, only the presence of water reed was significant for water total P, and only shoreline harnessing was significant for sediment total P (and correlated positively, Table 2, Table S2).

The different macrophyte indicators responded differently in the GLMs (Table 2, Table S2). Overall, variation in macrophyte mass, the lower vegetation limit, species richness and *Chara* abundance were strongly governed by the factor lake. This is likely due to the rich and abundant macrophyte beds in Lake Ohrid. The hypothesized change in predominant growth form among macrophytes with eutrophication was not clearly supported. We found mainly scatter versus PC1 (Fig. 3a) and no effect of P-load. When data were pooled into quartiles for PC1, quartile 3 had a maximum mean number of species and percentage of potamids, and a minimum percentage for elodeids, whereas the mean percentage of charophytes did not change (data not shown). Macrophyte species richness responded strongly to water level fluctuation and PC2 in the multiple regression without the factor lake (Table 2, Table S2, cf. Fig. 3b). Macrophyte mass also covaried positively with the presence of gravel beaches, water reed, and negatively with fetch. In the multiple regression, PC2, gravel beaches and water level fluctuation correlated with high biomass. For *Cladophora* mass a range of other factors

together were more important than the difference between lakes (Table 2, Table S2): fetch, PC2 (increased conifer and marshland), shore harnessing and gravel beaches, all covaried positively with *Cladophora* in the GLM, and water total P and water level fluctuation replaced the factor lake in the multiple regression. Also, *Chara* abundance corresponded significantly and negatively with water total P in the multiple regression, a pattern that disappeared with inclusion of the factor lake (Table 2, Table S2).

The diatom indicators - species richness and TDIL - were significantly different between lakes, but here other variables were also important (Table 2, Table S2). Interestingly, species richness increased significantly with urbanization (PC1, Fig. 3c), P run-off, fetch and water level fluctuation, but declined with PC2. The multiple regression produced largely the same results. TDIL covaried negatively with PC1 and with fetch both in the GLM and the multiple regression, whereas the factor lake was not significant.

Variation in benthic invertebrate abundance did show a significant between-lake difference. Abundance increased strongly with PC1 (urbanization, Fig. 3d), and with fetch. In contrast, fetch and water level fluctuation were significant in the multiple regression. Taxon richness differed between lakes and declined with PC1 (Table 2, Table S2). PC2 and water level fluctuation were significant in the multiple regression. We found that ASPT correlated negatively with sediment total P and differed between lakes, whereas water total P and water level fluctuation were significant in the multiple regression.

For some of our indicator variables the factor lake contributed substantially, whereas for others it contributed little to nothing (Table 2). The former was especially the case for water total P, sediment total P and ASPT, and less substantial but still sizeable for the lower vegetation limit, macrophyte richness, and the sum of *Chara* abundance. The factor lake was not significant for TDIL and invertebrate abundance. GLMs and multiple regressions overall included the same significant explanatory variables for diatom species richness, TDIL and *Cladophora* mass, whilst different sets of variables were significant in GLMs and multiple regressions for the other four macrophyte indicators and the three macroinvertebrate indicators (Table 2, Table S2). The predominant influence of the factor lake on concentrations of P in water and sediment makes these indicators of little use to describe a eutrophication gradient despite the gradient in loading, which corresponds with the finding of Schneider et al. (2020a). TDIL was related consistently and negatively to PC1, the urbanization gradient, and to fetch (Table 2, Table S2). This implies that fetch is a confounding factor in our data set for an assessment of the adverse combination of pressures related to increased urbanization along the shoreline. Fetch had a consistently positive effect on invertebrate abundance (Table 2, Table S2).

Since water level fluctuation did not vary within lakes, it could not be used to show any significant effect over and above the factor lake, but it was often significant in the multiple regressions. Its effects were negative for all macrophyte and invertebrate indicators, but positive for diatom species richness (Table 2, Table S2). The latter appeared to be most responsive to different explanatory variables, together with *Cladophora* mass (Table 2).

In overview, we see that variation in water and sediment P was mainly driven by differences between the lakes that were not picked up by our land use and shoreline indicators. For the diatom indicators, between-lake differences are important only for species richness but not for the eutrophication indicator TDIL, which was found to respond to increased urbanization (explains 26%, Table S2), and can be confounded by fetch (29%). The different macrophyte indicators show contrasting responses (Table 2), with different shoreline factors together being most important for *Cladophora*, but between-lake differences being most important for macrophyte mass, macrophyte species richness, *Chara* abundance and lower vegetation limit. Also, for the invertebrate ASPT the factor lake explained most (Table 2). For invertebrate abundance and taxonomic richness, however, the pattern is different, land use explained most variance (Table S2).
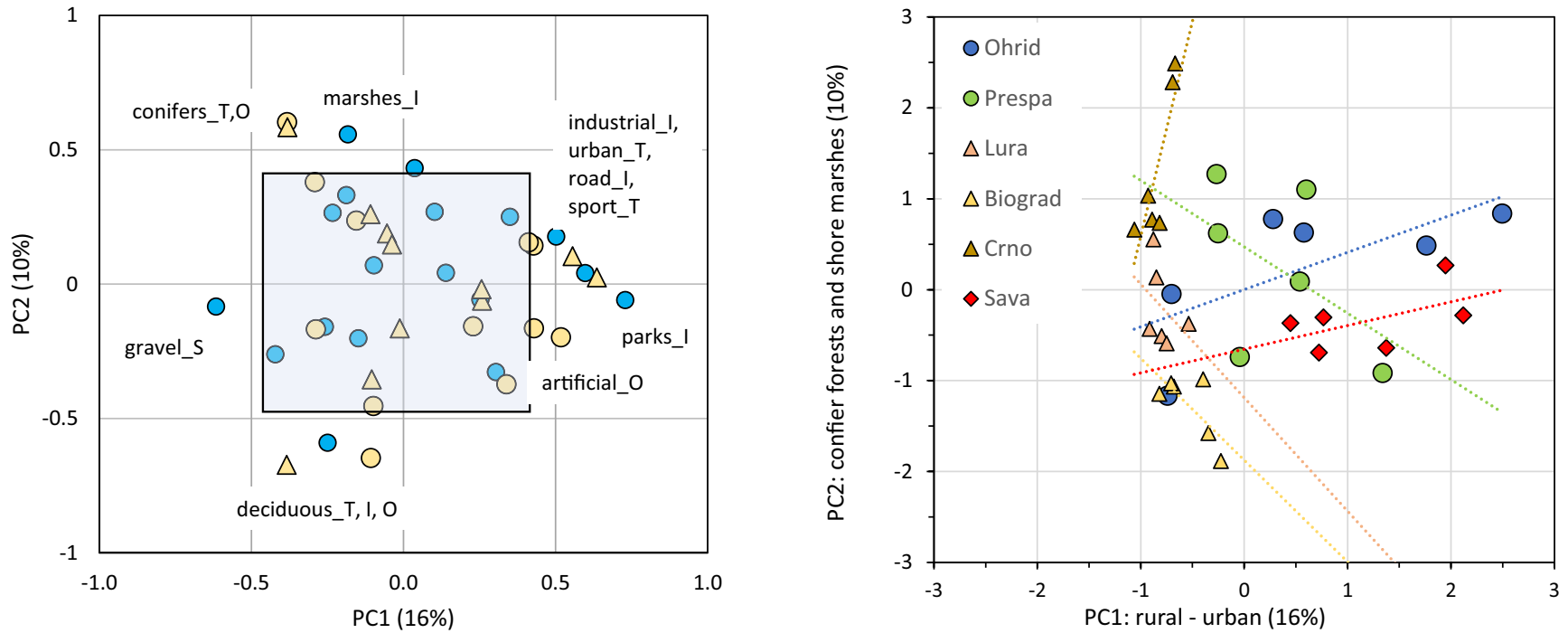
Fig. 2. PCA plot of land use in 10 ha CORINE trapezoids, in situ land use classification assessments in the immediate shoreline, and bands of 0–20 m and 20–100 m on land adjacent to each study station. Left displays the correlation coefficients of each variable with the first two principal components, and right is a scatter plot of the principal component scores for 6 stations and each lake. Left: Variables with correlation coefficients over 0.5 are considered to correlate significantly and indicated with a label, the transparent quadrat shades the area with correlations <0.5. Blue circles, yellow circles and yellow triangles as well as the capital affixes S, I, O, and T indicate immediate shore, inner littoral 0–20 m, outer littoral 20–100 m and LANDSAT trapezoid, respectively. A third component that explained 9% of the variance is not displayed. It covaried significantly ($r > 0.5$) with sandy beaches, complex agricultural land use in the trapezoids, and fruits and berries in the 20–200 m band. Right: Regression lines are illustrative of the trends within each lake. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Overall comparison of the results from the GLM (with lake as a random factor) and the multiple regression (without lake) summarized from Table S2. Explained variance and significant ($p < 0.10$) explanatory variables are reported, the latter with the sign of the relation ($-$, $+$).

| indicator	GLM r^2	GLM explanatory variables	Regression r^2	Regression explanatory variables
Water total P	0.83	Lake (69%), water reed ($+$), water level fluctuation ($+$), gravel, beach ($+$)	(0.28)	Whole model not significant ($p = 0.49$),
Sediment total P	0.50	Lake (60%)	(0.20)	Whole model not significant ($p = 0.46$)
Diatom species richness	0.87	Lake (27%), pc1 ($+$), pc2 ($-$), P runoff ($+$), water level fluctuation ($+$), fetch ($+$), shoreline harnessing ($-$)	0.80	pc1 ($+$), pc2 ($-$), P runoff ($+$), water level fluctuation ($+$), fetch ($+$), sediment total P ($+$)
TDIL	0.84	pc1 ($-$), fetch ($-$)	0.83	pc1 ($-$), fetch ($-$)
Macrophyte mass	0.78	Lake (13%), fetch ($-$), water reed ($+$)	0.74	pc2 ($+$), water level fluctuation ($-$), gravel beach ($+$)
Lower vegetation limit	0.78	Lake (18%)	0.63	pc2 ($+$), fetch ($+$)
Macrophyte species richness	0.92	Lake (11%), water reed ($+$), gravel beach ($+$)	0.82	pc2 ($+$), water level fluctuation ($-$)
Cladophora mass	0.94	Lake (3%), pc2 ($+$), shoreline harnessing ($+$), gravel beach ($+$), fetch ($+$)	0.92	pc2 ($+$), shoreline harnessing ($+$), gravel beach ($+$), fetch ($+$), water level fluctuation ($-$), water total P ($-$)
Sum *Chara* abundance	0.83	Lake (19%), sediment organic matter ($+$)	0.63	pc2 ($+$), water level fluctuation ($-$), fetch ($+$)
Mean invertebrate abundance at 2 m	0.86	pc1 ($+$), fetch ($+$)	0.82	Water level fluctuation ($-$), fetch ($+$)
Invertebrate taxon richness at 2 m	0.91	Lake (10%), pc1 ($-$)	0.85	pc2 ($+$), water level fluctuation ($-$)
ASPT	0.73	Lake (27%), sediment total P ($-$)	0.54	Water level fluctuation ($-$), water total P ($+$)
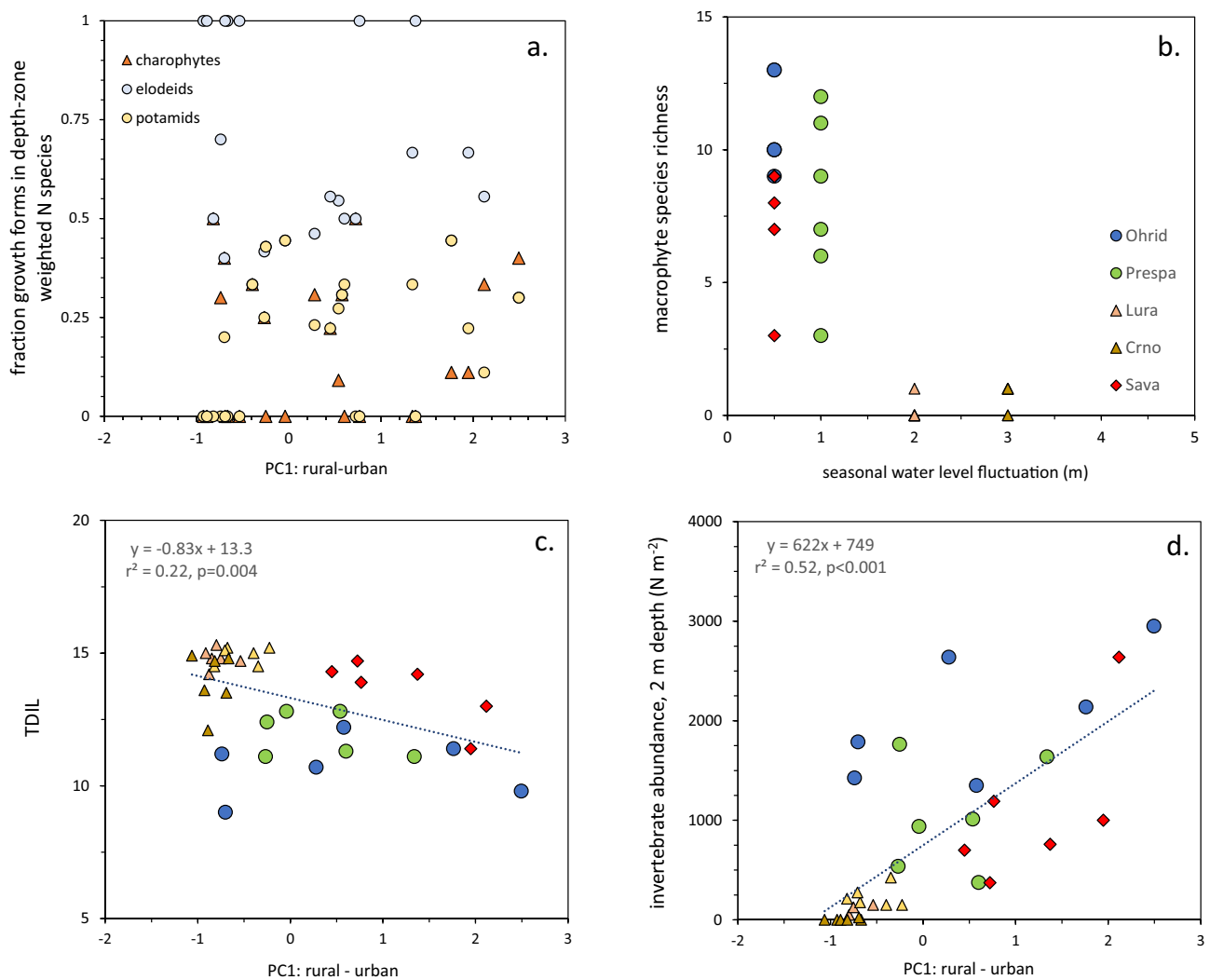
Fig. 3. Scatter plots of four selected biological indicators pooled across lakes versus a significant explanatory variable. In (a) the proportion of three growth form groups in the number of macrophyte species is plotted against PC1. In (b) a single, overall log-linear fit of macrophyte species richness versus water level fluctuation was significant, explaining 69% of the variance. In (c) the linear regression of TDIL versus PC1 is plotted, and in (d) the regression of invertebrate abundance against PC1 Is plotted.

4. Discussion

We observed substantial gradients across the six lakes in the indicators we used to reflect the three environmental pressures: eutrophication (P -load), hydro-morphological shoreline change, and altered water level fluctuation regimes. Also, our GLM models explained a substantial part of the variance in the biological response variables (73–94%, Table 2), which allows us to draw conclusions about the importance of the three different pressures. Importantly, since the land-use urbanization gradient (PC1) correlated with P-load, and especially since it correlated with TDIL, macroinvertebrate abundance and taxon richness, we can interpret this urbanization gradient to also reflect eutrophication.

For our macrophyte indicators, we found no direct relationship with eutrophication, but rather with hydro-morphological change indicators, and the factor lake was generally more important. This is likely because Lake Ohrid stood out with respect to macrophytes: it had the highest biomass, species richness, abundance of *Chara* and also *Cladophora*, and the deepest vegetation limit. Therefore, our six lakes did not provide a uniform gradient in macrophyte abundance or diversity (cf. Fig. 3b). With a much higher spatial and functional resolution or a very different analysis, Schneider et al. (2014) and Vermaat et al. (2020) show that the dense and extensive littoral macrophyte beds of Lake Ohrid protect the oligotrophic, 'inner' pelagic zone, from a substantial external nutrient load, which is reflected in the abundant presence of *Cladophora* in the upper littoral zone wherever the habitat is suitable, i.e. where there is hard substrate for attachment.

Diatom taxon richness increased with PC1 and P-run-off, whereas the eutrophication indicator TDIL decreased with PC1, though not with P-run-off (Table 3). This appears in contrast to the findings of Schneider et al. (2020a) but is likely partly due to the urbanization gradient replacing P-run-off, and partly to the multivariate nature of the current analysis. An increase in taxonomic richness of cobble-inhabiting diatoms with increasing urbanization may at first seem counter-intuitive but can be seen as an indication that our study lakes are not subject to very high nutrient loading. At low nutrient concentrations, diatom species richness has been shown to increase with increasing nutrient concentrations (Schneider et al., 2013), while at higher nutrient concentrations, diatom species richness declines with increasing nutrient concentrations (Weckstrom et al., 2007). This corresponds with the observation that the ranges of nutrient load and total P concentration in our study lakes are about half that reported in the literature (Smith et al., 2005; Poikane et al., 2014; Donohue et al., 2009). TDIL responded negatively to fetch. This could mean that fetch is a potentially confounding factor if TDIL is used without further consideration as an indicator of eutrophication, i.e. that wave-exposed sites could have a lower TDIL than sites which are less wave-exposed (see also Kelly et al., 2018).

For benthic invertebrates, an increase in abundance and a decrease in taxon richness along the urbanization gradient is interpreted as coupled with increased productivity, a trend which is consistent with the literature (e.g. Donohue et al., 2009; Pilotto et al., 2015; Johnson et al., 2018). We found no effect of hydro-morphological shoreline change on benthic invertebrate indicators in our study lakes, despite the considerable variation observed in shoreline change (Table 1). This is surprising and in contrast to the findings of, among others, Brauns et al. (2007), and Pilotto et al. (2015), but also of Jurca et al. (2021) who suggest that the negative effect of shoreline alteration on macroinvertebrate species richness could be stronger in oligo- and mesotrophic than in eutrophic sites. We speculate that the persistence of macrophyte beds across the observed range in shoreline alteration may contribute to the lack of responsiveness in macroinvertebrate indicators, because macrophyte beds are species-rich habitats for invertebrates (e.g. Rasmussen, 1988; Pilotto et al., 2015) and may act as refuges (Brauns et al., 2008), thereby masking potential effects of shoreline alteration. Remarkably, we found that the invertebrate index ASPT, which is considered to reflect a response to eutrophication or organic loading, responded negatively to water level fluctuation. With other words, a low score, indicating organic loading, could also be brought about by high water level fluctuation and an emerging littoral zone. Previous studies on benthic invertebrates and water level fluctuation (Rasmussen, 1988; Palomäki, 1994; Brauns et al., 2008) have not reported lower ASPT scores with higher water level fluctuations. Consequently, a potentially confounding effect of water level fluctuations on macroinvertebrate indicators must be considered in future assessments of lake ecological status, just as the possibly confounding effect of fetch on TDIL, the diatom indicator of eutrophication.

Due to the overlap of the factor lake and water level fluctuation, we could not formally separate these two. However, in our multiple regressions without the factor lake water level fluctuation was often significant and had a negative effect on macrophyte and *Cladophora* mass, as well as on all invertebrate indicators. This corresponds to results of Rørslett (1984), who found that large seasonal fluctuations in water level would compress the habitat available for submerged macrophytes. This direct effect on macrophytes as habitat may indirectly strengthen the effect on invertebrates (cf. Rasmussen, 1988). Contrary to all other effects (Tables 3, 4), water level fluctuation had a positive effect on diatom taxon richness. Possibly, a more complex interplay of colonization, duration of habitat availability and maybe grazing pressure on these epilithic diatom communities underlies this observed pattern (cf. Mason and Bryant, 1975; Vermaat, 2005). It may be, for example, that the shallow water cobbles we sampled had been submerged

Table 3
Relative importance of the three different pressures eutrophication, hydromorphological shoreline change and water level fluctuation based on the explained variance in the GLM and the multiple regressions (Table 2, Table S2). The urbanization gradient reflected in PC1 is interpreted to correspond with eutrophication.

Indicator	Eutrophication	Hydromorphological variation	Water level fluctuation[a]	Other
diatom species richness	pc1 + (10%) P-runoff + (26%)	Shoreline harnessing – (1%)	+ 36%	Lake (27%), fetch + (21%)
TDIL	pc1 – (26%)	-	-	Fetch – (29%)
macrophyte mass	-	Water reed + (8%) Gravel beach + (0%)	(-, 16%)	Lake (13%)
lower vegetation limit	-	-	-	Lake (18%)
macrophyte species richness	-	Water reed + (4%)	-	Lake (11%)
Cladophora mass	-	Shoreline harnessing + (6%) Gravel beach + (5%)	(-, 19%)	Fetch + (15%), pc2 + (6%), Lake (3%)
sum *Chara* abundance	Sediment organic matter + (0%)	-	-	Lake (18%)
invertebrate abundance	pc1 + (57%)	-	(-, 19%)	–
invertebrate taxon richness at 2 m	pc1 – (18%)	-	(-, 53%)	Lake (10%)
ASPT	Sediment tot P – (0%)	-	(-, 19%)	Lake (27%)

[a] Water level fluctuation in '( )' if only significant in the multiple regression, in the GLM its effect is covered by the factor lake; the explained variance estimate is to be interpreted as approximate as it is based on type I sums of squares.

Table 4
Hypothesized indicator responses to pressures and observed patterns.

Indicator group	Pressure	Hypothesized responses	Observed pattern confirmed?
Macrophyte	eutrophication	Less charophytes, more elodeids and potamids,	No, trend is not apparent
		Increased abundance of *Cladophora*	No, not more *Cladophora*
	Shoreline harnessing	Increased abundance of *Cladophora*	Yes, more *Cladophora*
		Change in relative abundance growth forms, less shallow-water species	Change in growth forms not seen
	Water level fluctuation	Compressed habitat, so less species, more small short-lived annuals, so less biomass	Yes, significantly less biomass
diatoms	eutrophication	TDIL score decreases	Yes, TDIL decreased with PC1
	Shoreline harnessing	Less, but specialized species	Yes, species richness declined
	Water level fluctuation	Less, but specialized species	No, species richness in fact increased
Benthic invertebrates	eutrophication	Increased abundance in response to productivity	Yes, abundance increased
		Shift in species composition: reduced richness	Yes, taxon richness declined
		ASPT score decreases	No, ASPT did not respond
	Shoreline harnessing	Reduced taxon richness	No response
	Water level fluctuation	Reduced richness	Yes, richness declined, but also abundance, and ASPT declined

sufficiently long for a rich diatom community to develop but not yet long enough for competitive species to become dominant (e.g. Passy, 2008).

Fetch interacted negatively with TDIL, and positively with diatom species richness, *Cladophora* mass, and invertebrate abundance, supporting the notion that it is important to address fetch separately in similar comparative analyses, both within and between lakes. Near-shore wave climate is an important factor structuring littoral habitats and benthic communities (Rasmussen, 1988).

Consistent covariance among the three indicator groups was limited. The specific answer to our second question (how strong is the covariation among the indicator groups?) is that only two pairs covaried clearly: the first pair is diatom taxon richness and invertebrate abundance, which both responded positively to the urbanization gradient reflected in PC1, but the former responded to several other factors, including shoreline harnessing, fetch and the factor lake (or water level fluctuation). The second pair is TDIL, the diatom-based index of nutrient load, and invertebrate taxon richness, which both responded negatively to PC1. A plausible explanation for this covariance is that the eutrophication gradient does not extend as far as elsewhere in Europe due to the observed moderate external loading and still functional retention mechanisms (Vermaat et al., 2020). Thus, increased nutrient availability may increase the available niche width for diatoms, and lead to increased productivity (Fairchild and Everett, 1988, Snyder et al., 2002, Vermaat,2005) and consequent increased invertebrate abundance (Mason and Bryant, 1975). However, the latter favors fewer, competitive invertebrate taxa, and the diatom community becomes dominated by indicators of higher nutrient availability (Hillebrand and Sommer, 2000), hence a lower TDIL (Stenger-Kovacs et al. 2007). This corresponds with earlier findings from Lake Ohrid (Schneider et al., 2014), and underlines that the use of different indicator groups will strengthen our understanding of the state of the lake and the underlying mechanisms.

The explanatory power of the factor lake varied among the different biological indicators. Hence, answering our third question (how important is the "unique" character of the individual lakes?), we argue that these lakes are 'unique to a degree.' This proportion never amounted to more than a third of the variance (Tables 2 and 3). This is notably so for four indicators: diatom species richness (27%), invertebrate ASPT (27%), the lower vegetation limit (19%) and the summed *Chara* abundance (19%). Similar breakdowns of variance have been published for littoral invertebrates: the contribution of the factor lake, due to natural spatial or morphological variation, varies widely (14–40%; Pilotto et al., 2015, Johnson et al., 2018). Our observations are within that range. Based on the significantly explained variance, we return to our first question (how much of the observed variance is explained by the different pressures?) and conclude that eutrophication, which we interpret from both the urbanization gradient and P-load, is likely more important in these lakes than direct hydro-morphological shoreline

change for diatoms and invertebrates, but that this is not apparent for the macrophyte indicators.

We now turn to our last question on generic inferences for lake water quality management in the Western Balkans. Our findings suggest that a gradient of increased urbanization of the shores corresponds to increased eutrophication. This likely includes other forms of pollution that we have not quantified, such as loading with easily degradable organic matter from domestic sewage, heavy metals and other persistent pollutants and microplastics (e.g. McGrane, 2016; Müller et al., 2020). This urbanization pressure had a strong effect on the relevant diatom indicator TDIL and on invertebrate abundance (Table 4). The effect was not so clear for macrophytes, where we did not find a trend towards a change in growth form from charophytes towards elodeids and potamids (cf Hilt et al., 2018; Poikane et al., 2018) or a change in species richness. This suggests that overall, whole-lake nutrient loads in these Western Balkan lakes may not have surpassed critical loads for the onset of algal blooms, because littoral vegetation is still functional as a buffer (cf Vermaat et al., 2020). Water transparency across four of the six studied lakes was not that low (spring median Secchi depth 3.9, range 2.4–15.2) allowing for the development of macrophyte beds, and likely also maintained by these (Vermaat et al., 2000, 2020). An alternative explanation may be that water level fluctuation overrules the potential effect of nutrient load: time to colonize frequently exposed littoral sites may be too short for the development of a more slowly growing macrophyte or macroinvertebrate community, while the smaller, fast growing (cf. Damuth, 2001) diatoms indeed react.

Based on our regression analyses, we suggest that water level fluctuation is likely to be equally important as eutrophication, but we could not formally separate it from the factor lake. Baumgärtner et al. (2008) suggest that natural water level fluctuation is highly important for the structuring of littoral invertebrate communities in large Lake Constance. One can argue based on island biogeography theory (MacArthur and Wilson, 1967) that it should have the strongest effect in smaller lakes, whereas in larger lakes the total size as well as variation in littoral morphology may allow for a buffering of habitat and thus eventual species loss in any of the indicator groups. Hydro-morphological change in these lakes appeared to have the least effect, contrary to findings by others (Pilotto et al., 2015; Miler and Brauns, 2020). This is likely due to the relatively modest proportion of shoreline that is modified in the studied lakes (cf. Table 1), but a direct comparison is complicated by the different ways in which shoreline modification is quantified (e.g. Brauns et al., 2007; Pilotto et al., 2015; Miler and Brauns, 2020; Jurca et al., 2021).

5. Conclusions

We suggest that eutrophication related to urbanization and water level fluctuation have more distinct adverse effects in these lakes than hydro-morphological shoreline change. We found that the indicators

based on diatom taxonomy were particularly responsive in a way that corresponds to earlier findings (Schneider et al., 2020a), whereas the observed patterns in benthic invertebrate indicators or macrophytes were less clear (contrary to e.g. Pilotto et al., 2015, Poikane et al., 2018). Finally, although lakes in the Western Balkans are comparatively rare, and some are to be considered unique based on their geological age and endemic biodiversity (notably Lake Ohrid), this did not prevent us from drawing general conclusions about pressures and their effects across these lakes. Our results suggest that our metrics can be applied in Western Balkan lakes, despite the high number of endemic species present in some of these lakes. We could indeed assess the relative importance of the pressures thought to cause changes in the different biological response parameters. We suggest that societal measures should focus on reducing nutrient load by addressing the drivers and sources of eutrophication, and on the causes of hydrological change that increase water level fluctuation, whilst preserving sufficient lengths of undeveloped littoral shoreline, in order to ensure good water quality in the long run.

CRediT authorship contribution statement

JEV and SCS conceived the idea for the paper; all discussed the concept and the possible structure of the paper; JEV, SCS and DH ran the statistical analyses and all discussed the outcomes; JEV wrote the first and second draft which all reviewed and commented on. All contributed to major parts of the field sampling and further processing and laboratory analyses of the samples.

Declaration of competing interest

We have no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.150160.

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