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Nutrient retention by the littoral vegetation of a large lake: Can Lake Ohrid cope with current and future loading?

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Abstract

Nitrogen and phosphorus budgets were compiled for the littoral (29 km^2) and pelagic (329 km^2) of ancient, deep, clear, and hard water Lake Ohrid (Albania and North Macedonia), to assess the importance of the littoral in nutrient retention. P originates mainly from domestic point sources (73%), for N this is karst seepage (50%). Total littoral loads are estimated at 1700 kg P and 23,200 kg N km^{-2} (area of littoral) yr^{-1}; net littoral retention is 31% ± 13% for P and 40% ± 16% for N, largely in the dense charophyte belt. P retention is mainly due to detritus burial, but also due to coprecipitation; N retention is due to both detritus burial and denitrification. A Monte-Carlo plausibility analysis balanced the budget by increasing nonconnected domestic household inputs (from 20% to 27% of external load), and decreasing pelagic sediment P burial by 27% and littoral denitrification by 25%. Scenario projections for 2100 corresponding to SRES A2 and B1 were linked to an AQUASIM lake ecosystem model. Under B1, the changes were small compared to the present. A2, however, led to a major reduction in precipitation, an increase in evapotranspiration, a reduction in river outflow (to ~ 20%), a doubling in P-loading, a drop in lake level of ~ 1.5 m, and a decline in the extent of the charophyte belt. Areal loading of the littoral would increase accordingly, but water transparency would not decline much. Also, the littoral vegetation will witness a shift in species composition, and an increase in filamentous *Cladophora* cover.

A buffering role for the littoral is generally not incorporated explicitly in whole-lake eutrophication studies of large, deep lakes (e.g., Vollenweider 1975; Schindler 2006; Scavia et al. 2014; Beutel and Horne 2018; Fink et al. 2018; but see Sachse et al. 2014). In contrast, studies on shallow lakes take littoral vegetation into account as an important element in nutrient dynamics (e.g., Jeppesen et al. 1999; Søndergaard et al. 2007). This implies that the possibly shifting share of littoral vegetation in whole lake nutrient budgets is ignored, despite Kalff's (2002, p. 295) suggested that "macrophyte beds … permit portions of the littoral … to serve as net sinks." Perennial charophyte beds, in particular, may have the potential to serve as nutrient sink, as they form dense carpets protecting the sediment from resuspension (Benoy and Kalff 1999; Vermaat et al. 2000), retain assimilated N during slow decomposition of the lower tissue (Rodrigo et al. 2007), and coprecipitate P with carbonates during photosynthesis which is then retained in the sediment (Kufel et al. 2013). Given the importance of light availability for the colonization depth of water plants (Chambers and Kalff 1985; Duarte and Kalff 1990; Schwarz et al. 2002; Søndergaard et al. 2013), its interplay with bathymetry can be expected to determine the extent of submerged vegetation (Kolada 2014; Sachse et al. 2014).

Indeed, in many large lakes where macrophytes have declined during eutrophication, load reduction programs have led to increased transparency, reduced plankton stocks, and often a recovery of macrophytes (Jeppesen et al. 2005; Hilt et al. 2010; Mueller et al. 2014).

Ancient, large, deep, and oligotrophic Lake Ohrid (shared between Albania and North Macedonia) has not lost its macrophytes, but is considered to be under threat of eutrophication (a.o. Matzinger et al. 2007; Schneider et al. 2014) due to a rapidly expanding urbanization (including tourism) and intensifying agriculture in its catchment. Paradoxically, this is not reflected in the phytoplankton composition of the open pelagic (e.g., Matzinger et al. 2007), though an increasing pelagic P concentration (from a historic ~ 1.3 mg m^{-3} to a "current" ~ 4.6 mg m^{-3}) and decreasing deep hypolimnetic

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Additional Supporting Information may be found in the online version of this article.

dissolved oxygen concentrations have been inferred from recent sedimentation records and recursive modeling (Matzinger et al. 2006*a*,*b*, 2007*a*). Schneider et al. (2014) observed higher total phosphorus concentrations in the near-shore littoral than Matzinger et al. (2007*a*) reported for the open pelagic, and observed high densities of the green alga *Cladophora* on hard substrates along the shoreline, together with other macrophyte, diatom, and macroinvertebrate taxa indicating eutrophication. These observations made Schneider et al. (2014) and Trajanovska et al. (2014) postulate that the littoral zone with dense macrophyte stands and filter-feeding benthic invertebrates could act as a phosphorus trap buffering the pelagic from eutrophication. The eutrophication model developed by Matzinger et al. (2006*a*, 2007*a*) for Lake Ohrid directly connected estimated external nutrient loads to the pelagic biogeochemical cycle, ignoring a potential buffering role of the littoral zone.

Matzinger et al. (2006*a*) reported a significant decline of water transparency between 1920 and 2005 (from 16.5 to 13 m, corresponding to a decline of 0.032 ± 0.019 m yr^{-1}). Accordingly, the maximum penetration depth of the *Chara tomentosa* belt in Lake Ohrid may also have crept up gradually. Stankovic (1960) reported that the "dense prairies of the *Chara* belt occur between 6 and 15–20 m," and more recently Trajanovska et al. (2004) reported a maximum depth of 18.5 m for Ohrid Bay. If the *Chara* belt acts as an important nutrient trap, and if a gradual upward narrowing of the belt occurs in correspondence with decreasing water transparency, then Lake Ohrid may be gradually on its way to a regime shift as has been observed in shallow (e.g., Janse et al. 2010; Hilt et al. 2018), as well as deep lakes (e.g., North American Great Lakes, Lake Constance; Auer et al. 2010; Stich and Brinker 2010; Depew et al. 2011; Bunnell et al. 2014). Such a regime shift including the hitherto unexpected disappearance of the *Chara* belt, and termination of its nutrient retention capacity, could possibly lead to a more distinct eutrophication and cyanobacterial dominance in the pelagic. Also, such a shift may be accelerated by climate change effects as postulated by Jeppesen et al. (2005), Wagner and Adrian (2009), and Mooij et al. (2009; but see Stich and Brinker 2010).

Here we estimate the nutrient retention capacity of littoral vegetation for Lake Ohrid, by compiling littoral budgets of nitrogen (N) and phosphorus (P). Based on these budgets, we address the question whether this lake ecosystem may be at risk of a regime shift by future societal and climate change. We estimate plausible, expected near-future changes in nutrient loading based upon two well-established International Panel for Climate Change, Special Report on Emission Scenarios (IPCC-SRES) scenarios of climate and societal change (e.g., Van Vuuren and Carter 2014; *see* "Methods" section below). We include both N and P in our assessment, although the published literature has focused on P (Matzinger et al. 2006*a*,*b*, 2007*a*; Schneider et al. 2014). We do this for two reasons: (1) Dominant sources of N and P are often different, and so are the pathways (e.g., Levine and Schindler 1992; Jeppesen et al. 2005), and thus different measures may be relevant. (2) More generally, pelagic phytoplankton may be limited by N or P, or both, depending on relative availability and stoichiometry of the algal community (e.g., Sterner 2008). Allen and Ocevski (1977) concluded from in situ bottle C^{14}-uptake bioassays with pelagic plankton in Lake Ohrid that P stimulated carbon uptake more often than N, but also Si and Fe were often found stimulatory. Increasing loads of both N and P may therefore have direct and indirect as well as interactive effects on extent, density, and community composition of littoral macrophyte beds, periphytic communities, and planktonic microalgae (reviewed in Phillips et al. 2016).

The littoral of a lake is composed of different interrelated subsystems which can be depicted as a set of stocks and fluxes in an annual mass balance. We use a simple breakdown (Fig. 1) of the littoral into three components: the sediment, the macrophyte vegetation, and the overlying water. The latter is connected to the open pelagic. This allows us to use the budget data from Matzinger et al. (2007*a*) and augment these with as yet unpublished data from Matzinger's field work and internal reports of the Hydrobiological Institute in Ohrid. Our research questions are: (1) How high is the current external load of N and P, and how much of it is retained annually in the littoral? (2) Based on plausible scenario projections, what would be the probable future nutrient loading, the extent and buffering capacity of the Chara belt, and consequent pelagic effects?

Methods

Study area

Lake Ohrid (Fig. 2) is located at 693 m a.s.l. in a tectonically active graben forming a steep valley surrounded by karstified Triassic limestone mountains up to 2300 m a.s.l. The lake is shared between Albania and North Macedonia. For a detailed description of its hydrogeology, limnology, and biodiversity, we refer to, for example, Stankovic (1960), Matzinger et al. (2006*a*,*b*, 2007*a*), Albrecht and Wilke (2008), Lindhorst et al. (2010), Matter et al. (2010), and Vogel et al. (2010). Currently, the littoral vegetation of Lake Ohrid is characterized by a discontinuous belt formed by patches of reed beds extending into the water (*Phragmites australis*, down to 1.5 m depth), extensive stands of submerged angiosperms (notably *Potamogeton perfoliatus*) in the shallow littoral down to about 4 m, and a largely continuous dense belt of *C. tomentosa* (from 4 m to about 11 m; Trajanovska et al. 2014; Trajanovska et al. pers. obs.). Maximum colonization depths for these belts in North Macedonia reportedly are 5 mfor Phragmites, 9 m for pondweeds, and 18.5 m for Chara (Talevska and Trajanovska 2019), but we use here more conservative median depths for the whole lake. *C. tomentosa* is wintergreen, and it shows a seasonal increase in green biomass in summer and a decline toward winter due to the gradual senescence at the bottom

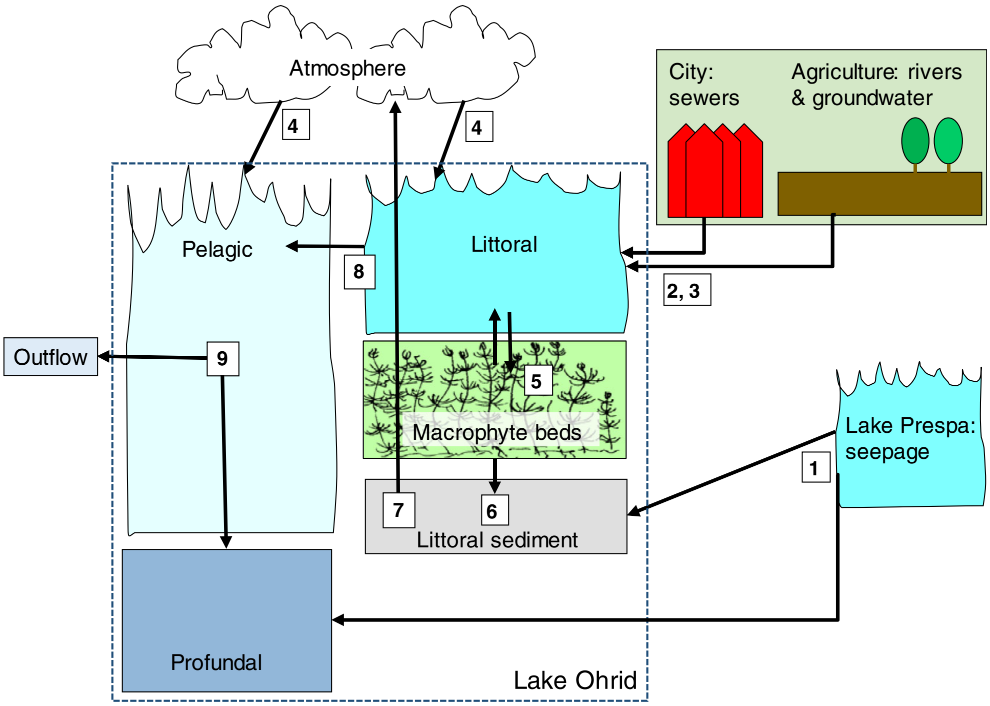

Fig. 1. Stocks and fluxes of N and P quantified for the littoral of Lake Ohrid. Fluxes 1–9 are discussed in the "Methods" section. "Budget components" and estimates are given in Table 1 and Supporting Information Table S1. The flux number coding corresponds with these tables. Note that areas are not to scale. [Color figure can be viewed at wileyonlinelibrary.com]

ends of the shoots (Trajanovska et al. 2004). *C. tomentosa* must have been abundant in Lake Ohrid for millennia, given its abundance as "larger intact *Chara* fragments" that have accumulated in deeper sediment strata down to ~ 90,000 yr BP in a sediment core taken at 32 m depth (Lindhorst et al. 2010).

Using spatial data from the bathymetric map in Schneider et al. (2014), we estimate that the littoral zone covered with more or less continuous macrophyte beds extending down to a depth of 11 m, covers 29 km^2 (8% of the total lake area) and has a volume of 0.16 km^3. The open pelagic has an area of 329 km^2. The pelagic photic zone, reaching down to 1/1000 light compensation depth (chosen instead of 1% following Matzinger et al. 2006*a*) at 50 m, has a volume of 16.5 km^3. The seasonally mixed layer extends to around 200 m depth, whereas the rest of the hypolimnion down to the maximum depth of the lake at 289 m is infrequently mixed. The lake is estimated to have a total volume of ~ 55 km^3 and a bulk hydraulic water residence time of 70 yr (Matzinger et al. 2006*a*). The catchment of Lake Ohrid is urbanized or under intensive cropping where the terrain allows this, or otherwise covered by forest and extensively grazed mountainous shrubs and grasslands. Particularly the eastern shore attracts substantial tourism, fanning out from the ancient town Ohrid. Matzinger et al. (2006*b*) report a resident population of ~ 174,000 and a summer season tourist influx of ~ 50,000 yr^{-1} for the whole catchment of Lake Ohrid including that of uphill Lake Prespa which is hydrologically connected to Lake Ohrid via seepage. Observed and perceived decline of Lake Ohrid's endemic trout, its endemic benthic invertebrate biodiversity and lake water quality in general have been subject of public concern. This has led to a number of conservation and sewage infrastructural improvement efforts, both in North Macedonia and Albania (Spirkovski et al. 2001; Nihon Suiko Sekkei co 2012).

Estimating the nutrient budget components

Approach

Overall, our approach was to first compile annual budget components for N and P. We then added plausible uncertainty estimates and carried out a Monte Carlo experiment to arrive at a balanced, that is, closed balance estimate. Assuming steady state, average annual nutrient inputs to and losses/outputs from Lake Ohrid can be considered equal:

$$\mathrm{Inp_{lit}} + \mathrm{Inp_{pel}} = \mathrm{Loss_{lit}} + \mathrm{Loss_{pel}} \tag{1}$$

where $\mathrm{Inp_{lit}}$ (kg yr^{-1}) is the total external nutrient input to the littoral (from karst seepage, domestic point, and various non-point sources), $\mathrm{Inp_{pel}}$ (kg yr^{-1}) is the total direct nutrient input to the pelagic (via atmospheric deposition and deep spring inflows), $\mathrm{Loss_{lit}}$ (kg yr^{-1}) is the nutrient loss from littoral, and $\mathrm{Loss_{pel}}$ (kg yr^{-1}) is the nutrient loss from pelagic (via outflow and net sedimentation). We will first explain how we derived the different balance terms, and then specify how we balanced

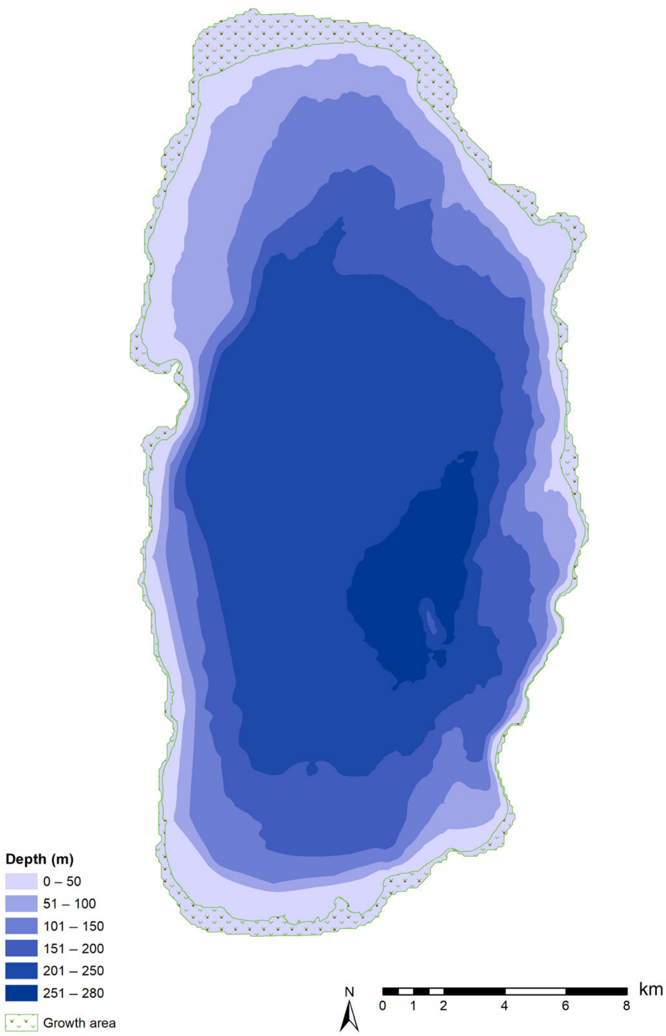

Fig. 2. Map of Lake Ohrid and its approximate littoral zone (growth area, 0–11 m depth). Bathymetric data reworked from Schneider et al. (2014).

the budgets. The main budget terms that we have quantified are illustrated in Fig. 1, and the literature data to quantify these terms are compiled in Supporting Information Table S1.

External loads to the littoral (Inp_{lit})

Our annual budget identifies four major inputs into the littoral of the lake (Fig. 1): (1) Seepage from the surrounding mountains including water derived from Lake Prespa; (2) Domestic and industrial sources summed from river loads that mainly drain urbanized parts of the catchment. This includes combined sewer overflows during intensive rainfall events and leakage and other failures of the sewage system; (3) Often more diffuse loading from agriculture, here mainly included in the load from those rivers draining agricultural land; (4) Atmospheric deposition.

Loss from littoral ($Loss_{lit}$)

In the littoral, part of the load is assimilated into living plant and periphytic biomass (component 5 in Fig. 1 and Table 1), part of the P is coprecipitated with carbonates onto the plants during photosynthesis in this hard water lake, and part of the N is denitrified in sediment or periphyton and disappears to the atmosphere as N_2. For the angiosperms, each winter the aboveground biomass decays. This detrital material is partly mineralized and released into the water column and partly ends as detritus in the sediment (component 6a, Table 1). The charophytes are wintergreen in Lake Ohrid, thus enhancing retention in the littoral sediment. The carbonate-bound P will largely settle and contribute to the local, underlying sediment (component 6b). How much of this sedimented matter will end up in the deep profundal is hard to judge but the low steepness of the slopes and the occurrence of a hummocky topography on the two terraces in Ohrid Bay ($\sim$ 30 m and $\sim$ 50 m, Lindhorst et al. 2010) suggests that this must occur with low frequency over longer time scales. For our annual budget, we therefore assume that the carbonate-bound P will remain trapped in situ in the littoral sediment and does not reach the pelagic. We assume that denitrification (7) is restricted to littoral sediments and periphyton because deep profundal waters lack nitrate and the hypolimnion has oxygen very close down to the sediment (Matzinger et al. 2006*a*).

External loads to pelagic (Inp_{pel})

The net annual pelagic load is composed of the proportion of the littoral load that is not retained plus the proportion of the decaying plant material that is mineralized (component 8). This term is inferred from the balance and not estimated from empirical data. In addition, atmospheric deposition and a small fraction of deep water spring inflows are assumed to reach the pelagic directly.

Loss from pelagic ($Loss_{pel}$)

Nutrients are lost from the pelagic by permanent burial (component 9a, Table 1) of biomass and coprecipitated P. Denitrification is assumed of minor importance given the low biomass input, and largely oxic conditions at the sediment–water interface. Nutrients also leave Lake Ohrid via its surface outflow Crn Drim (component 9b).

Estimation of plausible budgets and their uncertainty

The budget components (1–9) have been quantified based on empirical parameters from available published and unpublished data on Lake Ohrid and literature (see detailed assumptions and calculus in Supporting Information Table S1). Since all these parameters are empirical results, uncertainty of each individual parameter has been estimated in the form of standard deviations (SDs). To estimate the overall uncertainty in our budget results, parameters were randomly selected and simulated in a Monte-Carlo experiment with 10,000 runs using the R packages base and stats (*see* Supporting Information S2 and S3). For each run, parameters were selected assuming normal (or in some cases, log-normal) distribution from the estimated mean and SDs (see estimates in Supporting Information Table S2). However, selecting parameters within their estimated bounds does not necessarily provide plausible budgets. A particular problem lies in the separate quantification of all the budget components which leads to an over-parameterized balance that does not necessarily close for all combinations of parameter sets. Therefore, we added two requirements for the sampled parameter sets to avoid implausible combinations: (1) parameters with positive means need to remain positive (e.g., a negative denitrification rate is not plausible); (2) total directly calculated littoral nutrient loss (= $\mathrm{Loss_{lit}}$) needs to be within 20% of the total littoral nutrient loss calculated from the balance (= $\mathrm{Inp_{lit}} + \mathrm{Inp_{pel}} - \mathrm{Loss_{pel}}$, thus closing the balance) for both N and P. If any of these requirements was violated, the entire parameter sample was discarded. This—second—Monte-Carlo experiment was continued until a total of 10,000 runs fulfilled the above requirements. This constrained Monte-Carlo experiment may lead to a parameter fitting to the plausibility requirements with new (skewed) distributions around different means/medians than that made with the original parameter estimations (see results in Supporting Information S4).

Retention capacity

Apart from the actual budget components, the relative nutrient retention capacity η of the littoral vegetation of Lake Ohrid is of particular interest:

$$\eta = \frac{\mathrm{Loss_{lit}}}{\mathrm{Inp_{lit}}} \tag{2}$$

where $\mathrm{Loss_{lit}}$ (kg yr^{-1}) is the nutrient loss from littoral and $\mathrm{Inp_{lit}}$ (kg yr^{-1}) is the total nutrient inputs to the littoral, both from Eq. 1. Detailed balance equations and parameter ranges are all documented in the Supporting Information S2 and S3.

Scenario articulation

Matzinger et al. (2007) have carried out a scenario assessment combining a "current" baseline (zero temperature increase, loads of period 2001–2004) with three temperature increase regimes (0.01, 0.02, and 0.04°C yr^{-1}) and a halving or doubling of the current P load (50%, 200%). We aligned these to two of the four SRES global change scenarios which have become a benchmark for scenario analyses (A2 and B1, Busch 2006; Moss et al. 2010; Spangenberg et al. 2012). We assume that they correspond to two of the recent representative concentration pathway scenarios (RCP8.5 and 4.5, respectively; Van Vuuren and Carter 2014). Briefly, scenario A2 is considered to reflect a continued focus on fossil fuel-based economic development which we take to reflect a 4° world, whereas B1 reflects a strong focus on sustainability and renewable energy, or a 2° world (Busch 2006; Moss et al. 2010; Spangenberg et al. 2012). We used regional assessments for the southwestern Balkan from IPCCs TAR5 (IPCC 2013, Annexe 1, Figs. A1.40–43 and Table 14.1), and more detailed regional exercises (Tolika et al. 2012; Önol et al. 2014; Zanis et al. 2015). Our time horizon for the scenarios is 2100. For "current" annual precipitation over the catchment, we use 907 mm from Popovska (2007), whereas for Lake Ohrid we use 773 mm from Matzinger et al. (2006*a*). Evaporation and runoff are taken from Mimikou et al. (1999). Contrasting societal developments for A2 and B1 are deduced from Busch (2006), Westhoek et al. (2006), Spangenberg et al. (2012), and Vermaat et al. (2017). The scenario articulation for Lake Ohrid is summarized in Supporting Information Table S5. Our scenario articulation thus combines plausible projections for both changes in mean annual temperature and precipitation affecting the water balance, and the societal changes leading to changes in P load. Societal change projections corresponded well with the two different loading regimes (halving and doubling) applied by Matzinger et al. (2007), hence we did not have to rerun the AQUASIM-based lake ecosystem model and could directly use existing model output. The AQUASIM model is a one-dimensional biogeochemical lake model designed to quantify the dynamics of nutrients, oxygen, and plankton. It includes temperature, salinity, mixing (via a k-ε-approach), growth, respiration and mortality of phytoplankton and zooplankton, mineralization in the water column and at the sediment, nitrification, sedimentation, and phosphate uptake on sinking particles (Omlin et al. 2001; Matzinger et al. 2007). Full model equations are available in the web appendix of Matzinger et al. (2007). The effect of the scenarios on mean lake water level and outflow was estimated with a simple annual water balance, whereas effects of P load on light availability and depth penetration of the littoral charophyte belt were estimated from unpublished AQUASIM light attenuation output data (cf. Matzinger et al. 2007).

Results

Budget terms

Our budget compilations for the littoral area of Lake Ohrid show that domestic point sources are the main source of P (~ 73%), whereas seepage is the major source of N (~ 50%; Fig. 3a,d, Table 1—we present budget results after the plausibility constraining, *see* "Methods" section). Our calculations show that the external P-load to the lake littoral is about 1.7 g P m^{-2} (littoral) yr^{-1} and the current load from the littoral to the pelagic is 0.10 g P m^{-2} (pelagic) yr^{-1}. Equivalent estimates for N are, respectively, 23.2 g N m^{-2} (littoral) yr^{-1} and 1.2 g N m^{-2} (pelagic) yr^{-1}. Plant assimilation is the most important component in the gross uptake of both P and N in the littoral. The major pathway of net P removal is via burial of plant detritus whereas plant detritus and denitrification contribute approximately equally to net removal of N (Fig. 3b,c,e,f, Table 1). Due to the comparatively large contribution of denitrification, our estimated net retention η (related to the littoral inputs only, *see* Eq. 2) of N is higher than that of P: 40% ± 16% for N vs. 31% ± 13% for P (Fig. 4). Of the three

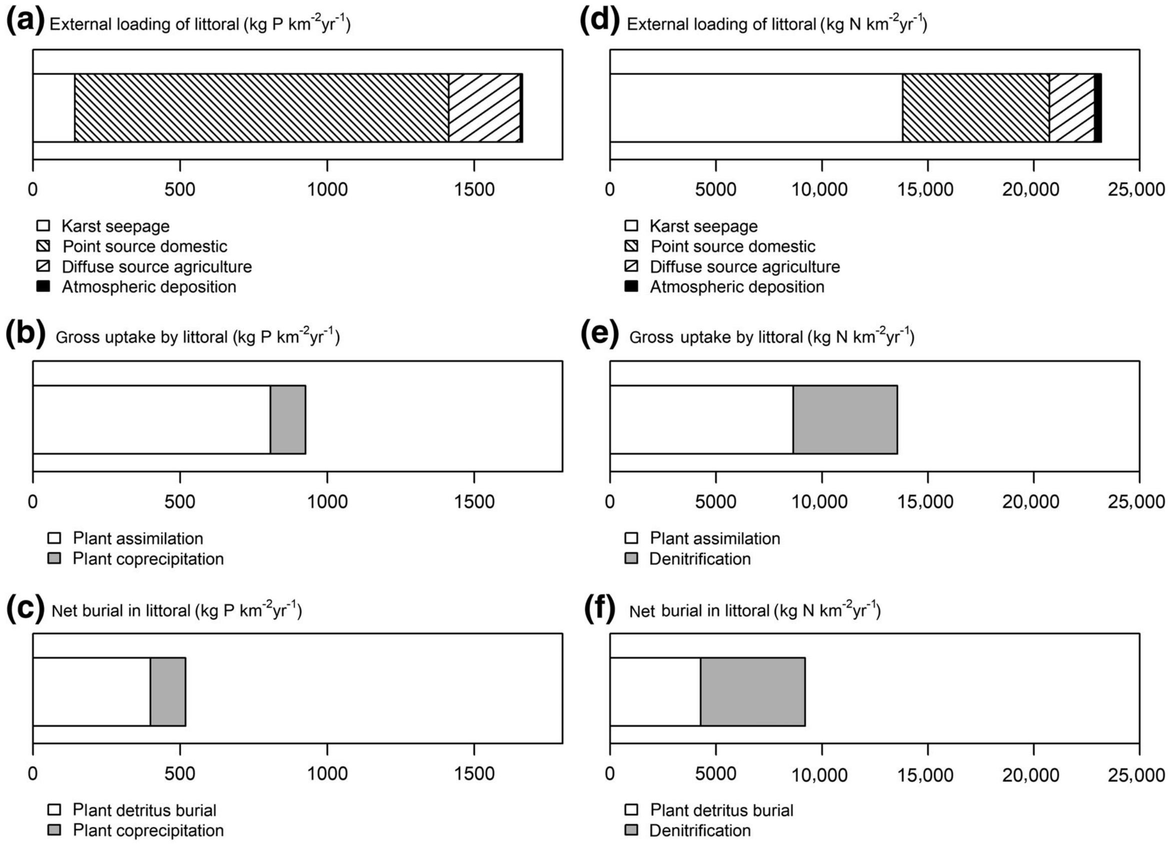

Fig. 3. Source apportionment of annual N and P loads per unit littoral area of Lake Ohrid (**a**, **d**), as well as gross and net littoral retention (**b**–**f**). Presented are annual means per area of littoral after Monte-Carlo fitting (*see* "Methods" section).

plant types distinguished, the *Chara* beds contribute most to littoral retention, particularly for N (65% of net retention) and if coprecipitation is included also for P (51%). This is due to their larger area and higher biomass in Lake Ohrid, not due to their higher specific nutrient content (Supporting Information Table S1). Direct inputs to the pelagic are limited and mostly due to atmospheric deposition for both N and P. Deep, pelagic sedimentation accounts for 64% of P and 56% of N of the total external load. Only 6% of P and 11% of N leave the lake via its outflow.

Uncertainty and plausibility constraining

Based on the Monte-Carlo distributions of the different load terms (indicated by SDs in Table 1), we estimated the relative contribution of the different balance terms to overall uncertainty, a value that combines influence and uncertainty of a balance term. On the input side domestic point sources dominate, making up 98% and 42% of uncertainty in total inputs for P and N, respectively. For N, karst seepage contributes a second substantial part (36%) to input uncertainty. On the loss side, uncertainty in the P balance is dominated by pelagic sediment loss (74%) and littoral detritus burial (23%). Uncertainty in N loss is mostly influenced by denitrification, plant detritus burial, and pelagic sedimentation with relative contributions of 53%, 18%, and 25%, respectively.

It is important to note that the a priori expert estimates of the different budget components (Supporting Information Table S1) did not meet the second plausibility constraint (i.e., closing the balance). The application of the two constraints to our Monte-Carlo experiment led to limited changes in the parameters, affecting only the following 5 (out of 39) parameter estimates by 10% or more. External inputs were increased via atmospheric deposition for N (+11%), Albanian Rivers for P (+16%) and mainly via the share in wastewater from nonconnected inhabitants (from 20% to 27%). On the loss side pelagic P sedimentation (−27%) and notably denitrification (−25% from 15.0 to 11.2 mg N m^{-2} d^{-1}) have been reduced. Overall, the changed parameters are well within their expected a priori ranges. Detailed results on parameter distribution are presented in Supporting Information S4 and S6.

Scenario outcomes

Application of the sustainability oriented B1 scenario led to only very limited changes in the water balance, and included a presumed 50% reduction in nutrient load to the lake. Thus, under B1, we expect the lake water to become even clearer

Table 1. Balanced nitrogen and phosphorus budgets after Monte-Carlo consistency simulation regarding the net balance terms from Eq. 1. See "Methods" section for the approach used. Balance terms are numbered in correspondence with Fig. 1 and Supporting Information Table S1.

	P ($t\ yr^{-1}$)		Percentage of total P loads		N ($t\ yr^{-1}$)		Percentage of total N loads	
Balance term	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
External loading to littoral (Inp_{lit})								
(1a+b) Karst seepage and other springs	4.1	0.8	8.1	2.2	400.1	67.2	50.0	10.2
(2) Point sources domestic	36.8	9.6	72.8	23.5	200.9	72.4	25.1	9.5
(3) Diffuse source agriculture	7.1	1.1	13.9	3.4	61.8	27.4	7.7	3.5
(4) Atmospheric deposition	0.2	0.0	0.4	0.1	9.0	3.8	1.1	0.5
Total	48.2	9.7	95.2	26.4	671.8	102.6	84.0	16.0
External loading to pelagic (Inp_{pel})								
(4) Atmospheric deposition	2.1	0.4	4.2	1.1	102.2	42.9	12.8	5.6
(1c) Deep spring inflow	0.3	0.1	0.6	0.2	25.4	9.3	3.2	1.2
Total	2.4	0.4	4.8	1.2	127.6	43.9	16.0	5.8
Net littoral loss ($Loss_{lit}$)								
(6a) Plant detritus burial	11.6	5.4	22.9	11.5	124.0	48.7	15.5	6.3
(6b) Plant coprecipitation	3.4	1.3	6.8	2.9	—	—	—	—
(7) Denitrification	—	—	—	—	142.7	84.1	17.9	10.7
Total	15.0	5.6	29.7	12.4	266.7	97.2	33.4	12.7
Net pelagic loss ($Loss_{pel}$)								
(9a) Sediment burial	32.2	9.8	63.6	22.8	445.5	57.7	55.7	9.6
(9b) Lake outflow	3.0	1.6	6.0	3.3	84.0	21.8	10.5	3.0
Total	35.2	9.9	69.6	23.7	529.5	61.7	66.2	10.8

(K_d decreases from 0.16 to 0.14), which will likely lead to a downward expansion of the *Chara* belt, hence a larger total area of the vegetated littoral. Our projection for A2 (fossil fuel-oriented economic growth), however, leads to a substantial reduction in rainfall and an increase in evapotranspiration together with a doubling in P-load (Table 2). This is estimated

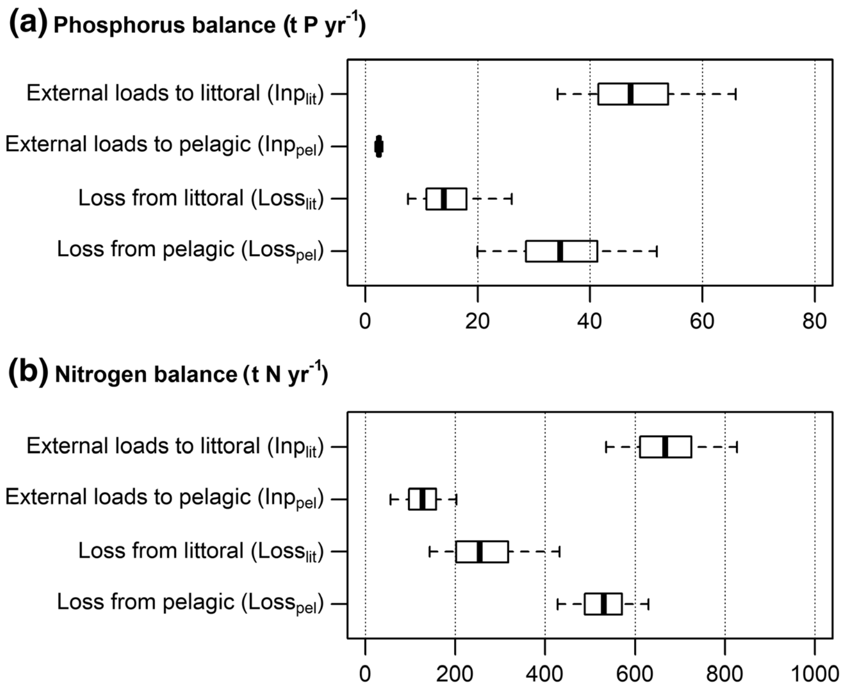

Fig. 4. Lake phosphorus (**a**) and nitrogen (**b**) balances, showing terms from Eq. 1. Boxes contain 50% and whiskers 90% of data. Data presented after Monte-Carlo fitting (see "Methods" section).

Table 2. Scenario outcomes for A2 and B1 in 2100 compared to the recent past (~ 2000–2010). Water balances are estimated from the numbers in Supporting Information Table S2; light climate data are derived from unpublished results from AQUASIM runs done for Matzinger et al. (2007).

Scenario	Recent past	A2	B1
Water balance (million m^3 yr^{-1})			
In: Rain	278 (773 mm)	204	260
Summer rain	103	48	92
Winter rain	175	156	168
In: Run-off rivers	281	225	267
In: Seepage inflow	636	235	514
SUM IN	1195	663	1031
Out: Evapotranspiration	410 (1145 mm)	533	451
Out: Outflow river Crn Drim	785 (25 m^3 s^{-1})	130 (4 m^3 s^{-1})	580 (18 m^3 s^{-1})
SUM OUT:	1195	663	1031
Underwater light availability			
Light attenuation coefficient (K_d, m^{-1}, ±SD over modeled depths and months)	0.16±0.03	0.18±0.03	0.14±0.02
Secchi depth (m) estimated from 1.58/K_d (ratio as in Matzinger et al. 2006*a*)	9.7	8.9	11.3
Percentage surface light available at 11 m depth (current conservative estimate of the lower limit of the *Chara* belt)	17	14	22
Depth with 10% of surface light (10% is conservative value of light requirement of Chara, range 5–10, Middelboe and Markager 1997, Schwarz et al. 2002)	14.4	12.8	16.4

to cause a drastically reduced mean annual outflow (4 m^3 s^{-1}, about 20% of current flow), and it is likely that the river would stop flowing during a considerable part of a much drier and warmer A2 summer in 2100. A crude estimate of the lake water level based on this water balance suggests an approximate drop in lake level of around 1.5 m. The projected doubling in P-load under A2, however, will probably not be fully reflected in P concentrations in the pelagic surface layer due to reduced mixing with higher temperatures (total P concentrations change from 1.8 to 2.7 mg-P m^{-3}; Matzinger et al. 2007), lake phytoplankton stocks, and light attenuation (Table 2). Hence, depth penetration of the littoral *Chara* beds will likely not be reduced substantially, and a drop in lake level will then lead to a parallel downward migration of the *Chara* belt, since sufficient light will remain available at the lower end of the belt (Table 2). Due to Lake Ohrid's bathymetry however, this will lead to a substantial areal reduction of the *Chara* belt, to approximately 19 km^2, which together with the doubled loading would increase the areal loading to an estimated 5.1 g P m^{-2} (littoral) yr^{-1} or 0.3 g P m^{-2} (pelagic) yr^{-1} (assuming an area-proportional reduction in littoral retention).

Discussion

Compiling the budgets and uncertainty

We have constructed a detailed budget breakdown for both N and P which allowed us to carry out a source attribution and include assessment of littoral retention by vegetation and sediment. The combination of (1) empirical data to set up reasonable ranges of balance terms with (2) a constrained Monte-Carlo experiment to close the balance has worked well and led to a plausible nutrient balance, which considers uncertainty, while keeping all parameters well within their expected empirical range.

Our assessment suggests that the largest uncertainties are contributed by external (littoral) loadings both for N and P, underlining the difficulty and importance of load estimates. Constraining the budget with "common sense" restrictions led to an increase in the share of wastewater from unconnected households but also in the load terms from Albanian rivers, all highly uncertain parameters that were based on few sampling campaigns and expert knowledge. Though the absolute numbers may still be uncertain, the plausibility testing indicated that our initial nutrient input estimates were generally too low. In turn, our initial loss estimates proved to be too high. In particular, littoral denitrification rates and pelagic P sedimentation have been reduced after the constraining (nutrient loss reduced by 40 t N yr^{-1} and 12 t P yr^{-1}, respectively, see also Supporting Information Table S6), and this is also plausible given their high contribution to overall uncertainty. The relative uncertainty of the single budget components in Table 1 varies between 26% and 118% (expressed as 2SDs). Most uncertain estimates with 2SDs > 90% are the P flux in the lake outflow, denitrification and P plant burial.

Particularly the latter two are important, as these are also the largest contributors to net littoral retention (Fig. 3, Table 1). This suggests that a conservative low-end estimate of these retention processes should accompany our overall final budget estimates (Fig. 3, Table 1), which supports the effects of the constraining. It also implies that empirical field assessments of these processes would be highly relevant.

A necessary point of caution is the fact that our budgets are compiled as annual aggregates, and hence lack any finer temporal resolution. For example, temporal mismatches between short-term peak loading and seasonally reduced buffering by vegetation could thus lead to a systematic overestimation of littoral buffering. However, we have grounds to think this is not a major issue here. First, since the main source of N is karstic seepage (Fig. 3), we assume that this will not rapidly bypass the littoral. Second, domestic sources are most important for P, and these are entering lake Ohrid mainly through rivers (20 ton P, Supporting Information Table S1) which have their peak flow in April and May (Matzinger et al. 2006a), when also the charophytes expand their new shoots (Trajanovska et al. 2004), or through slow continuous seepage (27 ton P).

Littoral and pelagic loading

It is noteworthy that phosphorus loading of Lake Ohrid can be attributed mainly to domestic sources (73%), whereas the nitrogen load derives from karst seepage (50%) and only second from domestic point sources (25%). The sources of this seepage nitrogen likely are atmospheric deposition and Lake Prespa, and possibly diffuse domestic nitrate leaching which does not reach the streams flowing into Lake Ohrid. Compared to literature, the current external area-normalized littoral P load (1.7 g P m^{-2} littoral yr^{-1}) is close to a critical load of 1–2 g P m^{-2} yr^{-1} we derive from model outcomes for well-flushed lakes with depth over 5 m in Janse et al. (2008) and Sachse et al. (2014). Expressed per total lake area the load is still comparatively low (0.10 g P m^{-2} pelagic yr^{-1}, below the critical load of 0.2 proposed for Lake Ohrid's depth and flushing rate by Lee et al. 1978). For comparison, Lake Constance has been recolonized by charophytes over extensive areas after the whole-lake loading had been reduced to 0.41 g P m^{-2} pelagic yr^{-1}. The littoral zone thus currently copes with a high external loading, likely by a combination of a high assimilation capacity during the growing season combined with a delayed loss to the pelagic, and subsequently to the hypolimnion, a well as littoral sediment burial. The latter two are both likely to be permanent.

Overall, our estimates suggest that net littoral retention (31% ± 13% of external loads to littoral for P and 40% ± 16% for N, or 518 kg km^{-2} yr^{-1} and 9197 kg km^{-2} yr^{-1}, respectively; Table 1) is considerable, buffering the open pelagic and reducing the net load. Thus, the littoral of Lake Ohrid indeed performs an important regulating ecosystem service as postulated by Schneider et al. (2014) and Trajanovska et al. (2014). The major littoral retention mechanisms for nitrogen and phosphorus are different. For phosphorus, the major mechanism is detritus burial, whereas for nitrogen detritus burial and denitrification contribute approximately equally (Table 1). Our retention estimates due to plant assimilation are similar to those estimated for dense *Chara hispida* beds in a Spanish hard water lake by Rodrigo et al. (2007; net evergreen plant and detritus retention ~ 4300 kg N km^{-2} yr^{-1}, our estimate for this term is 4275 ± 1680 kg N km^{-2} yr^{-1}).

Annual net P losses from the pelagic to hypolimnetic sediment and river outflow are about 35 ± 10 tons P yr^{-1}. This is approximately equal to the 33 ± 11 tons P yr^{-1} which enters from the littoral plus the 2.4 ± 0.4 tons P yr^{-1} external loads directly to the pelagic (Table 1). This steady state may well be augmented by the infrequent complete overturns redistributing P-richer bottom waters upward in the pelagic water column (Matzinger et al. 2007). Unpublished pelagic nitrate profiles (from campaigns reported in Matzinger et al. 2007) suggest similarly higher nitrate concentrations in the deeper pelagic particularly in autumn (60–100 μg N L^{-1}), but lower values in summer in the upper pelagic (< 20 μg N L^{-1}). The molar total N/total P ratio changes from 168 in the shallow littoral (0.5 m water depth) to 54 in the deeper open pelagic (Matzinger et al. 2007; Schneider et al. unpublished), suggesting strong but decreasing P limitation (cf. Kolzau et al. 2014) when going from the shallow littoral, to deeper pelagic waters, and a stronger littoral retention of N than P, which corresponds with our estimates.

Our conclusion that littoral vegetation has an important role in the N and P budgets, supports the argument of Benoy and Kalff (1999) that "an understanding of whole-lake functioning requires explicit consideration of littoral zones." In Lake Ohrid, the littoral vegetation covers 8% and 0.3% of the entire lake area and volume, respectively, but retains about a third of the external nutrient loading, while it processes (gross removal, Fig. 3) ~ 50% of the total external load before this reaches the pelagic. Areal loss rates are ~ 5 (P) and ~ 7 (N) times higher in the littoral compared to the pelagic. It is likely that this buffering capacity can be generalized to other large and deep lakes (e.g., Salmaso et al. 2007), where water quality improvement after eutrophication abatement measures has led to a recolonization by charophytes (Azella et al. 2014; Murphy et al. 2018). Indeed, processes in the littoral may account for the faster than expected P sedimentation during "oligotrophication" of four Swiss lakes (Mueller et al. 2014). We posit that eutrophication abatement programs should include littoral processes in their analysis also for large and deep lakes, and littoral areas of large lakes should have conservation priority, not only for their own sake, but also for whole lake management purposes. The focus should probably be on relatively shallow shelves down to 30 m (approximate maximum vegetation depth in very clear lakes; Schwarz et al. 2002, see also the next section), which historically may have had charophyte belts, but the absolute bathymetry of each individual lake is the ultimate determinant here (Kolada 2014).

Risk of a future regime shift for Lake Ohrid

Our scenario analysis shows limited change relative to the current situation for our articulation of the B1 scenario, but substantial changes in water balance for A2 leading to a water level drop of about 1.5 m. A doubling of the current P-load under A2 toward 2100, however, is projected to have a limited effect on pelagic algal abundance and light attenuation (Table 2).

Water transparency is likely the main proximate factor driving charophyte depth penetration (Chambers and Kalff 1985; Duarte and Kalff 1990; Schwarz et al. 2002; Søndergaard et al. 2013) also in Lake Ohrid, hence we may extrapolate from observations in many other large and deep central European lakes (Fig. 5), which have gone through a period of eutrophication control and large-scale charophyte re-establishment. The pattern (Fig. 5) suggests that depth penetration of charophytes relates curvi-linearly to Secchi depth. However, the change in penetration depth between 5 and 15 m Secchi transparency is not steep (Fig. 5, comparable to Middelboe and Markager 1997 and Schwarz et al. 2002), supporting the result of the ecosystem model. Our estimate for the scenario A2 suggests a continued decline in transparency (Table 2), but light availability still appears sufficient throughout the charophyte belt. We therefore argue that a doubled external loading of Lake Ohrid will likely only have a limited effect on the depth distribution of the *Chara* belt. However, since this belt will move downward together with the projected lowering of the water level of about 1.5 m, we have estimated that its total area will substantially decline from 29 to 19 km^2 due to the lake's bathymetry. As a consequence, our estimate of the areal P load of the vegetated littoral increases to 5.1 $g P m^{-2} yr^{-1}$, which is substantially beyond the upper end of a critical range of 1–2 $g P m^{-2} yr^{-1}$ (cf. Janse et al. 2008; Sachse et al. 2014) where shallower or smaller lakes would shift to algal dominance and lose their submerged vegetation. Here, however, the overlying littoral water is not isolated from the open pelagic, and light attenuation will likely not increase, as the AQUASIM modeling suggests. Hence, composition of the littoral vegetation will likely change toward increased dominance by taller pondweeds and elodeids (cf. Kolada 2014), periphyton on the macrophytes and *Cladophora* cover will increase, the latter as observed in the American Great Lakes (e.g., Auer et al. 2010; Depew et al. 2011). Hence, we argue that the hydrological effect of a "4° world" grasped in the A2 scenario will most likely lead to a reduced areal extent of the vegetated littoral due to lake bathymetry and a shift in littoral plant community composition toward species which are more tolerant to eutrophication.

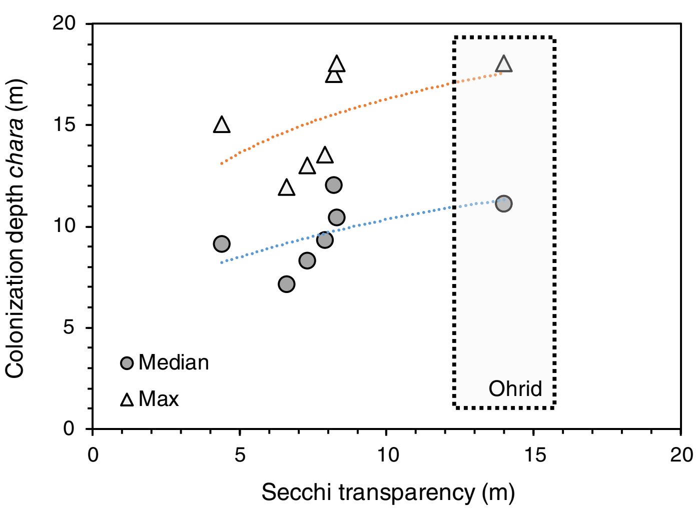

Fig. 5. Depth distribution of charophyte beds in deep central European lakes as a function of Secchi depth. Data often from the period of re-establishment after implementation of eutrophication abatement programs. Sources: Aquaplus (2010, 2012); Barbier and Quentin (2016); Bauer et al. (2011); Bolpagni et al. (2013). Lakes: Lake Constance Obersee and Untersee, Lake Geneva, Lago di Garda, Lake Lucerne, Lake Zurich. Data Lake Ohrid: STAR WALK project field work 2016. Fitted curves are not significant, but are included to indicate a trend.

One may speculate how strong the retention capacity of the reed belts in the upper littoral of Lake Ohrid would have been if their extent had not been strongly reduced by the expansion of residential and recreational shoreline occupation (cf. Vermaat et al. 2016). The remaining stands have a high biomass and nutrient content of which a considerable proportion is retained during winter in the extensive rhizome network. Also, *Phragmites*-dominated wetlands have high rates of denitrification and carbon sequestration (e.g., Olde Venterink et al. 2006), hence their retention potential is likely high. In our budget model, *Phragmites* shows 11 and 3 times higher areal retention of P and N, respectively, than *Chara* or *Potamogeton*, which underlines this potential.

Although our estimations suggest that also the extreme A2 scenario will likely not lead to a shift toward dense pelagic algal blooms in Lake Ohrid, there are enough other reasons to keep nutrient inputs at a low level. The first reason lies in the littoral area itself. The observed shift to more eutrophic species close to polluted river mouths (Schneider et al. 2014) may also affect the endemic littoral plant and animal communities of Lake Ohrid (e.g., Hauffe et al. 2011). Second, Matzinger et al. (2007) showed that, together with global warming, even a slight increase in productivity may lead to a reduction or complete depletion of dissolved oxygen below 250 m depth, which in turn may jeopardize the endemic deep-dwelling organisms and deep-spawning fish species. Third, one can speculate from the present study that nutrient loadings to the pelagic cannot only increase from activities in the catchment but also from destruction of littoral vegetation. Any shoreline development which affects the extent and vigor of the littoral vegetation will also enhance the load of the pelagic. Conversely, restoring destroyed littoral areas (both *Chara* belts and reed sections) could be an effective measure to protect the pelagic. Unfortunately, given the current increase in tourism on Lake Ohrid, the destruction of littoral areas may turn out to be an important threat for the littoral biodiversity of this unique lake—a pressure which we have not included in our AQUASIM modeling and nutrient budgets.

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Conflict of Interest

None declared.

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