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EDITED BY

Xiufeng Zhang,
Jinan University, China

REVIEWED BY

Yali Tang,
Jinan University, China
Marcus W. Beck,
Tampa Bay Estuary Program,
United States

*CORRESPONDENCE

Katrin Teubner,
Katrin.Teubner@univie.ac.at

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Macrophyte habitat architecture and benthic-pelagic coupling: Photic habitat demand to build up large P storage capacity and bio-surface by underwater vegetation

Katrin Teubner^{1*}, Irene E. Teubner², Karin Pall³, Monica Tolotti⁴, Willi Kabas⁵, Silke-Silvia Drexler⁶, Herwig Waidbacher⁶ and Martin T. Dokulil⁷

¹Department of Functional and Evolutionary Ecology, Faculty of Life Sciences, University of Vienna, Vienna, Austria, ²Department for Application Architecture and Development, Zentralanstalt für Meteorologie und Geodynamik (ZAMG), Vienna, Austria, ³Systema GmbH, Vienna, Austria, ⁴Research and Innovation Centre, Fondazione Edmund Mach, S. Michele all'Adige, Italy, ⁵Department of Limnology and Bio-Oceanography, Faculty of Life Sciences, University of Vienna, Vienna, Austria, ⁶Department of Water, Atmosphere and Environment, Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Sciences, Vienna, Austria, ⁷Research Department for Limnology, University of Innsbruck, Mondsee, Austria

Macrophytes play an important role in shallow lakes if large standing crop can be achieved. Here we stress the role of submerged macrophytes for benthic-pelagic coupling in the shallow oxbow lake Alte Donau (Austria) during restoration triggered by sufficient light availability (12% surface ambient light, photic_{>12%} depth, $Z_{optimum}$) in both, the benthic and the pelagic habitat. Focusing on $Z_{optimum}$, rather than on minimum light requirement (euphotic depth), seemed to be more meaningful to follow the macrophyte development. After phosphate precipitation treatment, the photic_{>12%} pelagic habitat accounted for more than half of the total water volume in summer, while the achievement of the same photic_{>12%} conditions for half of the total sediment surface area was delayed by 8 years. A delay of light exposure on the lake bottom area compared to the lake water volume is given by the basin morphometry, but the time span that is required for passing this delay depends on the efficiency of restoration measures. The 8-year delay for Alte Donau means that lake restoration focusing on macrophyte re-establishment was difficult to stimulate due to insufficient light exposure at the lake bottom. A further increase of photic_{>12%} conditions to more than 3/4 size of both pelagic and benthic habitat, however, eventually stimulated sustained macrophyte growth. With the onset of this large macrophyte biomass yield, the phosphorus storage pool of submerged macrophytes exceeded the annual peak concentration of total phosphorus of the whole lake water by about one order of magnitude for the first time. Further, the submerged macrophyte bio-surface exceeded the size of lake bottom surface, also by about one order of magnitude. Our results support that macrophytes can act as a significant sink of phosphorus by retaining this nutrient at least during the growing season. We

further see the immensely large macrophyte bio-surface as a vast spatial dimension for an additional habitat for freshwater biota. Therefore, we conclude that mature submerged macrophyte formations need to be considered not only as biomass yield, but create a unique macrophyte habitat architecture as a third main component in the network between benthic (lake bottom) and pelagic (lake water) habitat.

KEYWORDS

lake restoration and management, eutrophication, aquatic vegetation, water transparency, Secchi depth, underwater light climate, photic hypsographic curve

Introduction

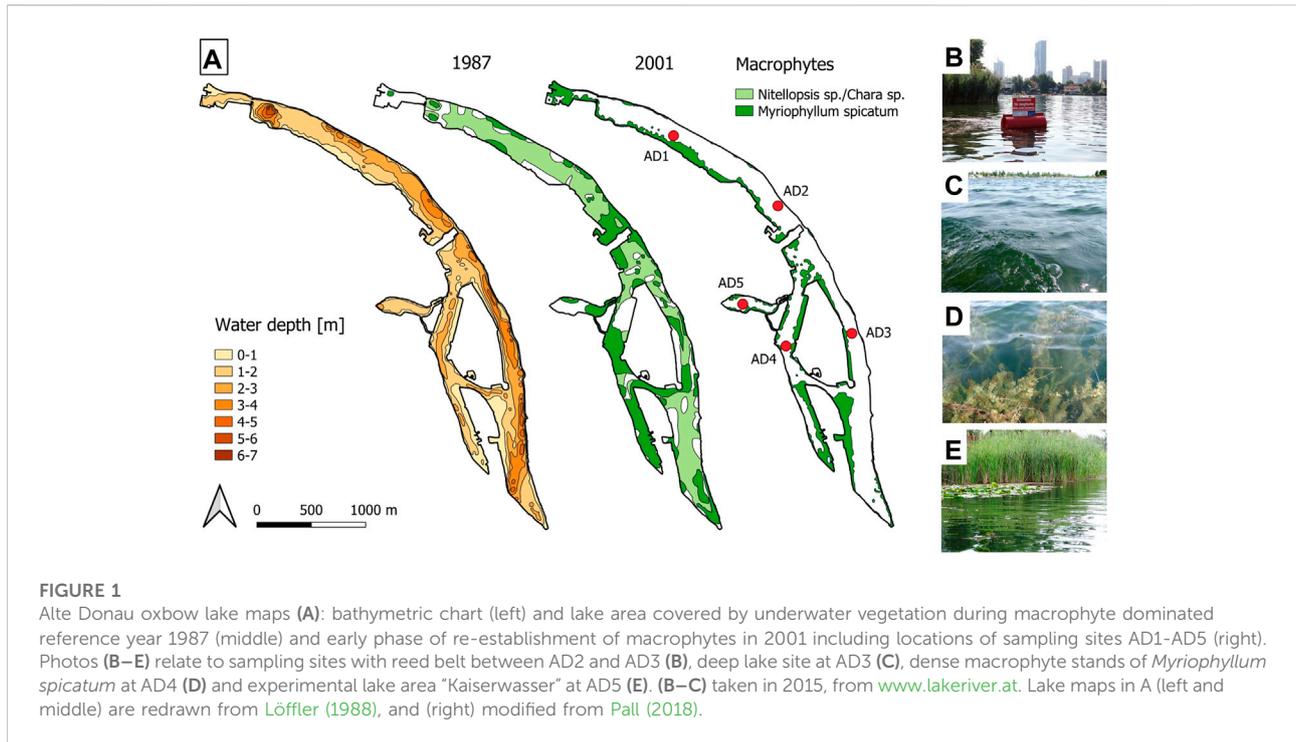
Benthic-pelagic coupling addresses any form of exchange between these two spatially different habitats (Vadeboncoeur et al., 2002; Gyllström and Hansson, 2004; Søndergaard et al., 2005; Ferreira et al., 2018; Urrutia-Cordero et al., 2020; Mei et al., 2021). Even if studies about benthic-pelagic coupling go back to early work in aquatic sciences (e.g., Johnson and Wiederholm, 1992; Gyllström and Hansson, 2004), a broader emphasis is put today on this issue in view of anthropogenic pressure and climate change (Griffiths et al., 2017; Ferreira et al., 2018; Urrutia-Cordero et al., 2020; Zhang et al., 2021). In the present study, we stress the role of submerged macrophytes for benthic-pelagic coupling in a shallow oxbow lake triggered by sufficient light availability.

According to Puche et al. (2021), the connectivity of “macrophyte-meadows” is mediated by primary producers and herbivores to both, the benthic and the pelagic habitat. This implies that “underwater meadows,” which are often categorized as being part of the benthic habitat (“benthic macrophytes”), should not be strictly assigned to either one of the two habitats. Macrophytes play a crucial role in particular in shallow lakes, however, their settlement on lake bottom depends on water transparency (Istvánovics et al., 2008; Jůza et al., 2019; Chorus et al., 2020; Dubey et al., 2021; Zhang et al., 2022). Therefore, macrophyte meadows are not obligate habitats such as the benthic and the pelagic zone in shallow lakes. They are more specific to lake ecology and thus less often studied than benthic or pelagic issues. Unlike small benthic organisms or flat mats of algal filaments, which live in the close vicinity of the lake bottom, underwater meadows, such as in Alte Donau, build a thick layer of 0.5–1.20 m height (Löffler, 1988). Mature macrophyte meadows of dense stands of charophytes or vascular plants build their own unique habitat architecture (Hacker and Steneck, 1990), often characterized by an underwater canopy including (1) a large interstitial water volume between thallus or plant shoots and (2) an immensely large bio-surface formed by charophyte thalli or vascular plant shoots. In case of macrozoobenthos studies, this specific habitat is commonly named “phytal” (Hacker and Steneck, 1990; Eidinger, 2018; Janecek et al., 2018).

In Alte Donau, the shallow oxbow lake of the presented study, high macrophyte yields have been recorded twice: firstly, in the mesotrophic reference year 1987, when dense charophyte meadows covered almost the whole lake bottom and were dominated by *Nitellopsis obtusa*. Secondly, in the period from 2004 to 2019 after the re-settlement of macrophytes due to lake restoration, when a high macrophyte yield could be accomplished again. With the re-establishment of macrophytes, the vascular plant *Myriophyllum spicatum* had become the dominant species, while charophytes were relatively sparse (Pall, 2018; Teubner et al., 2020). Although various vascular plant species and charophytes were planted during lake restoration, *M. spicatum* grew fastest and its canopy formation did not allow any other macrophytes to spread out spatially in Alte Donau (Pall, 2018). This macrophyte species often succeeds after being planted by macrophyte management (Yu et al., 2016; Gao et al., 2020). *M. spicatum* can also be the most abundant vascular submerged aquatic plant in natural habitats, i.e., in large lakes, along whole rivers and across biogeographical regions (Lake Vörtsjärv: Feldmann and Nöges, 2007; Danube River: Janauer et al., 2021; from temperate to tropical freshwater ecoregions due to broad thermal tolerance: Lind et al., 2022).

The macrophyte development is mainly controlled by underwater light climate (Istvánovics et al., 2008; Jůza et al., 2019; Baart et al., 2010; Dubey et al., 2021; Zhu et al., 2021). Therefore, in the present study about the emergence of macrophytes and benthic-pelagic coupling, we focus on light availability along the benthic and pelagic habitat. We analyse the progression of the size of the photic benthic and pelagic habitat, respectively, and how their extensions are spatially linked to each other.

In a previous study about the long-term restoration development of Alte Donau, we underscored water transparency as a socio-ecological indicator for urban waters. Water clarity can be also used as key parameter for bridging the criteria of ecosystem service supply and sustainable ecosystem health (Teubner et al., 2020; Teubner et al., 2021), which is most applicable for assessing the ecosystem services of waters in urban areas (e.g., Kumar and Shekhar, 2021; Cui et al., 2022). In the present 28-year study, we re-assess the underwater light climate for



macrophyte growth by retrieving underwater light attenuation from Secchi depth (z_{Secchi}). Keeping in mind that macrophytes are building up their own habitat architecture (Jeppesen et al., 2012), the present study aims at underscoring their ecological role beyond the macrophyte yield. As macrophytes are known to (1) stabilize pelagic phosphorus concentrations at low level in shallow lakes, and to (2) provision additional structure for settlement of other organisms, our benthic-pelagic coupling study is underpinning the role of these two aspects.

Methods

Site description and sampling sites

The oxbow lake Alte Donau (Figures 1A–D), part of the capital city Vienna, comprises two main impoundments, the north basin (sampling site AD1, AD2) and south basin (sampling sites AD3, AD4), and a small appendix, Kaiserwasser (AD5, Figure 1A). Although the reed vegetation along lake shores have also been restored (Figure 1E), the focus in the present study about benthic-pelagic coupling is on submerged vegetation (Figure 1D). Regular sampling for water chemistry (total phosphorus, TP; chlorophyll-a, Chl-a; dissolved organic carbon, DOC), water temperature (surface water temperature, SWT; depth integrated water temperature, WT) and Secchi depth (z_{Secchi}) was conducted at the three main sampling sites (AD1, AD3 and AD4) in the years 1987 and 1993–2019. Underwater

light profiles of Photosynthetically Active Radiation (PAR) measured with a 4π quantum sensor (LI-COR, Teubner et al., 2020) were conducted at AD2 (1997–2000).

Mesotrophic reference condition, eutrophication and restoration schedule over 27 years

The mesotrophic cyprinid-state of Alte Donau in 1987, characterized by dense meadows of underwater vegetation mainly of harophytes (biomass contribution: 74% of tons dry weight (DW) and 77% of tons fresh weight (FW), respectively), is described by a multidisciplinary author consortium in Löffler (1988). Even though first signs of increasing nutrients, a slight macrophyte decline, and other aspects of habitat deterioration related to recreational use were critically documented at that time, recent studies (e.g., Dokulil et al., 2018a; Teubner et al., 2020, 2021), as well as the present study claim that the year of 1987 describes reference conditions. An intensive multidisciplinary study started again with nutrient enrichment from 1993 onwards (Dokulil et al., 2018a). The hypertrophic situation with algal turbidity (cyanobacterial blooms, e.g., of *Cylindrospermopsis raciborskii*) (stage 1) is documented for 1993 and 1994. In-lake restoration treatment started with chemical RIPLOX-precipitation (phosphate precipitation with iron chloride and sediment oxidation with nitrate; Rippl, 1978) in 1995 and 1996, and resulted in a prompt drop of summer

phytoplankton (1995–2000, stage 2). Years 2001–2006 were dedicated to the re-establishment of macrophytes (stage 3) followed by the stage of “sustained restoration development” (2007–2019, stage 4). Further details about the long-term restoration measures in the years 1993–2014 most relevant for the present study are available for water chemistry in Donabaum and Riedler, (2018), for phyto- and zooplankton in Teubner et al. (2018a, b), for macrozoobenthos in Janecek et al. (2018), and macrophytes and helophytes in Pall (2018) and in Pall and Goldschmid (2018). Time series data plotted in this study do not only present a more recent development in Alte Donau until 2019 but also go far beyond aspects shown in Dokulil et al. (2018a, longest time series ends there in 2014).

Lake morphometry and photic hypsographic curve in view of underwater light availability

The depth contour lines of lake morphometry refer to <https://data.wien.gv.at>. The mean depth of Alte Donau ($z_{mean.depth}$) is 2.4 m, the maximum depth ($z_{max.depth}$) extends to 7 m, the ratio $z_{mean.depth} : z_{max.depth}$ is 0.34 (without the small area of a man-made deep hole the ratio is between 0.4 and 0.5; the lake bottom is at 149.8 m above the Adriatic Sea). According to calculations of the hypsographic curve using QGIS 3.16, the lake sediment area (709578 m², considers the slope of the lake basin) is 422 m² larger than the lake water surface area and the lake water volume is 3761950 m³. Usually, hypsographic curves display the morphometric depth-area relationship (e.g., Håkanson, 1977; Bragg et al., 2003; Hickley et al., 2003; Finstad et al., 2014). They often show the cumulative lake area at a given lake depth, i.e., as an increase of lake area along depth, summed up from the bottom to the surface since water fills up in a geological hole. The present study, however, aims at assessing light availability along strata of the water body and at the sediment surface of the lake bottom. Therefore, the cumulative percentage of water volume and sediment area, respectively, is cumulated from the lake surface down to the lake bottom, following the propagation of sun light which is attenuated along deeper strata in the water body (thus named “photic hypsographic curve” in our study, see also graphical presentation in our study). We further assessed conditions for sufficient light availability at water strata and on sediment area, i.e., the exposure to at least 12% lake surface ambient light (Supplementary Material_1, Figure S1), which is assumed to be supportive for optimum growth of primary producers, such as pelagic and benthic microalgae and macrophytes (see also method section “water transparency”). We further define from the photic hypsographic curve the water volume exposed to at least 12% surface ambient light as photic_{>12%} benthic habitat. In analogy, the lake sediment area exposed to at least 12% surface ambient light is the photic_{>12%} benthic habitat. In case of time series plots about the progression

of photic habitats in our study, we calculated the size for both photic_{>12%} habitats on the time resolution of biweekly data (see method section “statistical treatment of time series data”) and applied a spatial depth resolution of 0.10 m for $z_{optimum}$.

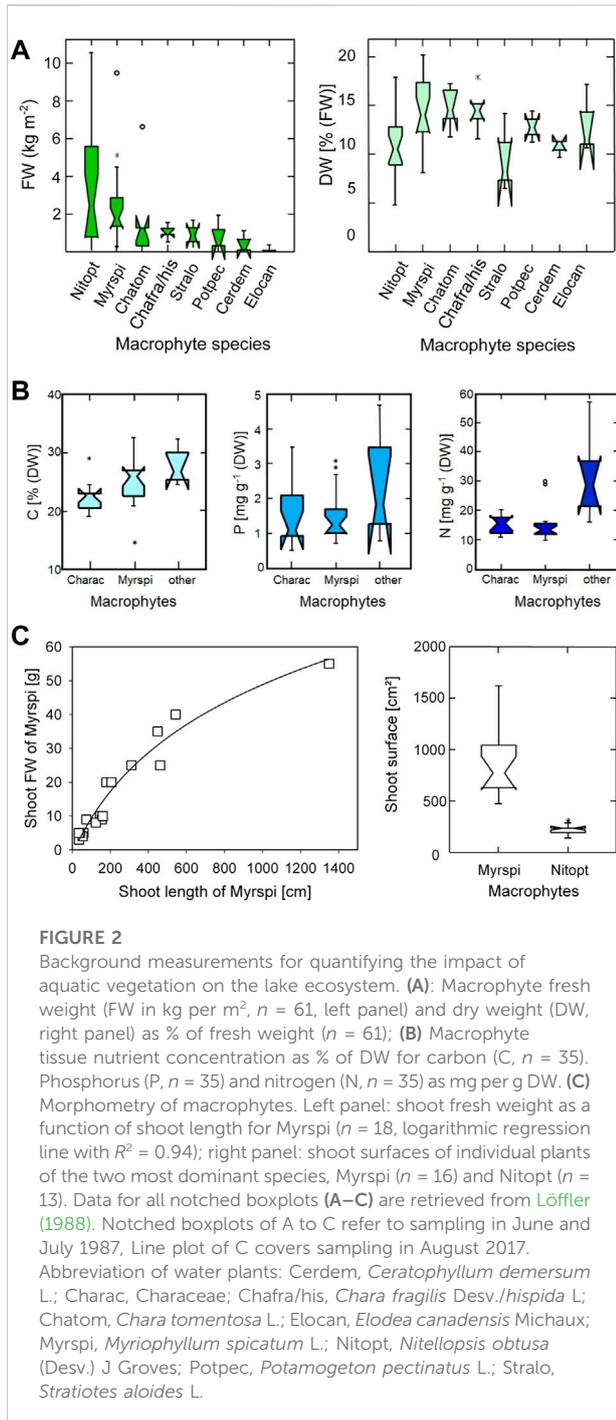
Concentration of TP, the response to this total pool of phosphorus by algal development (algal biomass estimated by Chl-a concentration), and followed up alterations of water turbidity (estimated by z_{Secchi}), are common criteria for trophic classification schemes. Water depth of ambient light supporting optimum growth of primary producers, here expressed by $z_{optimum}$, decreases with increasing trophic state in Alte Donau from mesotrophic ($z_{Secchi} = 5.5\text{--}2.5\text{m}$, $z_{optimum} = 8.9\text{--}3.4\text{m}$) to moderately eutrophic ($z_{Secchi} = 2.5\text{--}1.5\text{m}$, $z_{optimum} = 3.4\text{--}2.5\text{m}$), and further to highly eutrophic ($z_{Secchi} = 1.5\text{--}1\text{m}$, $z_{optimum} = 2.5\text{--}2.0\text{m}$) and hypertrophic ($z_{Secchi} < 1.0\text{m}$, $z_{optimum} < 2.0\text{m}$) (trophic classification scheme refers to ÖNORM M6231, 2001; see also Teubner et al., 2018a, Teubner, 2000). The corresponding $z_{optimum}$ was calculated from underwater light attenuation (k_{PAR}) retrieved from spring data with the equation in Supplementary Figure S2B (left-middle panel; spring is commonly used for trophic classification schemes).

Water transparency expressed by z_{Secchi} , k_{PAR} and $z_{optimum}$

The seasonally different background of light attenuation refers to the seasonal time-lag between concentration development of Chl-a and DOC in Alte Donau. A seasonal loop pattern is thus found when plotting k_{PAR} against Chl-a, DOC and z_{Secchi} , respectively, as described in the Supplementary Figure S2A. Equations for retrieving k_{PAR} [m⁻¹] from z_{Secchi} [m] by linear regression thus vary among seasons. The respective equations that are used in this study are as follows (details see Supplementary Material S2 and Supplementary Figure S2B):

$$\begin{aligned} \text{Winter } k_{PAR} &= -0.5151 \cdot \ln(z_{Secchi}) + 1.156 \\ \text{Spring } k_{PAR} &= -0.4518 \cdot \ln(z_{Secchi}) + 1.0129 \\ \text{Summer } k_{PAR} &= -0.6148 \cdot \ln(z_{Secchi}) + 1.1964 \\ \text{Autumn } k_{PAR} &= -0.6178 \cdot \ln(z_{Secchi}) + 1.2233 \end{aligned}$$

Teubner et al. (2020) used underwater light attenuation to identify three depth layers of specific ambient light requirements for photosynthetic domains of phytoplankton and submerged macrophytes: (1) z_{eu} , euphotic depth at 1% surface ambient light as minimum light requirement for phytoplankton growth, (2) $z_{macrophytes}$, maximum macrophyte colonization depth at 3% surface ambient light referring to minimum light requirement for macrophytes, and (3) depth of optimum light requirement of phytoplankton empirically indicated by an epilimnetic peak at 12% surface ambient light (Teubner et al., 2004). The latter is defined in the present study as $z_{optimum}$ (Supplementary Material



S1 and S2), assuming that 12% surface ambient light refers to optimal growth conditions for all underwater primary producers, i.e., algae and macrophytes. In addition, we focus in the present study on $z_{optimum}$, while neglecting the depths of the minimum light requirement for phytoplankton and macrophytes, respectively, as both seem ecologically less important in Alte Donau.

The depth of 12% of surface ambient light, $z_{optimum}$, is calculated from k_{PAR} as follows:

$$z_{optimum} = \frac{(\ln 100 - \ln 12)}{k_{PAR}} = \frac{2.120}{k_{PAR}}$$

The percentage of surface ambient light at Secchi depth z_{Secchi} ($I_{Z_{Secchi}}$) derived from k_{PAR} is:

$$I_{Z_{Secchi}} = e^{(\ln 100 - k_{PAR} \times z_{Secchi})} = 100e^{-k_{PAR} \times z_{Secchi}}$$

In analogy, the percentage of surface ambient light at mean lake depth ($I_{Z_{mean.depth}}$) is:

$$I_{Z_{mean.depth}} = e^{(\ln 100 - k_{PAR} \times z_{mean.depth})} = 100e^{-k_{PAR} \times z_{mean.depth}}$$

Macrophyte biomass yield and phosphorus nutrient-pool

Lake macrophyte biomass was estimated by echo-sounding of the whole lake (Löffler, 1988; Jäger et al., 2004; Pall, 2018) each year, the identification of species and collection of plant material for lab analysis by scuba-diving. In more recent years, the yield by underwater mowing was used to verify biomass estimates from echo-sounding. Macrophyte surveys relate to the aboveground biomass during peak growing seasons (summer surveys) and were considered as proxy for annual yield of the whole water basin throughout this study. In the reference year of mesotrophic state in 1987, charophytes were dominant and contributed to about three quarters of the total macrophyte DW biomass, while *M. spicatum* (and further spermatophytes of less importance) to the remaining one quarter (Löffler, 1988). In 1993, when macrophyte biomass was very low under hypertrophic conditions, the portion of charophytes was still high (90% *N. obtusa*) (Pall, 2018). In years of significant re-establishment of macrophytes, however, *M. spicatum* became the most dominant species from 2005 onwards, e.g., contributing about 90% to total biomass in 2014 (further details see Pall, 2018). These changing proportions between charophytes and *Myriophyllum* were taken into account for converting DW to FW of macrophyte biomass and vice versa (Figure 2A, left panels) and for calculating the nutrient content of macrophyte tissues (Figure 2B) according to Löffler (1988) (phosphorus content for *M. spicatum*: mean 1.54 mg g⁻¹(DW), median 1.21 mg g⁻¹(DW) and for charophytes: mean 1.51 mg g⁻¹(DW), median 1.11 mg g⁻¹(DW)), plant cover height and bio-surface of macrophyte plants. Fresh weight and nutrient content of macrophyte tissues were analysed from mono species plant samples which were prewashed with water (Löffler, 1988).

Stimulation of vernal macrophyte development by short-term water-level draw-down in spring was first tested in 2002 and then introduced on a regular basis from 2003 onwards as a macrophyte management measure in Alte Donau. Concurrently,

mowing in summer 2003 started removing macrophyte biomass during the growing season to some extent. The mowing program has been intensified since 2018, after 3 years of particularly high macrophyte biomass (2015–2017).

Data about the phosphorus concentration in sediment cores and the phosphorus release from sediment during hypertrophic state (1994) are provided in [Supplementary Material S3](#).

Macrophyte bio-surface

Determining the macrophyte bio-surface for the whole lake aimed at estimating (1) the potential for nutrient uptake via the thalli or shoots in addition to the rhizoids or roots, and (2) the macrophyte capacity of providing phytal habitat for invertebrates. The bio-surface was calculated from the total biomass of the macrophytes, their growth height and their surface per growth height. According to [Löffler \(1988\)](#), the mean plant shoot length in summer for *M. spicatum* is 192 cm (median: 172 cm, $n = 16$), and thalli length for charophytes 97 cm (median: 77 cm, $n = 12$; *N. obtusa*, *Chara tomentosa*). The bio-surface for *Myriophyllum* (4.5 cm² per cm shoot length) is higher than for charophytes (3.6 cm² per cm thalli length, [Löffler, 1988](#)). Accordingly, stands covered with *M. spicatum* provide a much higher surface area per m² sediment area, than charophytes, as shown for individual plants ([Figure 2C](#), right panel). The shoot fresh weight as function of shoot length for *M. spicatum* is shown in [Figure 2C](#) (left panel, mean: 0.085 g cm⁻¹, median: 0.078 g cm⁻¹, $n = 18$). The length of shoots is measured with a ruler. The shoot fresh weight is captured as macrophyte displacement volume (e.g., [Christie et al., 2009](#); [Nagengast and Kuczyńska-Kippen, 2015](#)), i.e., by measuring the difference of water volume with and without plant shoot in a graduated measuring cylinder (conversion: 1 ml macrophyte shoot displacement volume = 1 g fresh weight of macrophyte shoot). Estimating the displacement volume is a standard method for estimating phytoplankton biovolume or biomass from microscopical counting (using cell dimensions for calculating the cell-biovolume, e.g., [Rott, 1981](#); [Rott et al., 2007](#)) using the same conversion (1 cm³ phytoplankton biovolume = 1 g phytoplankton biomass).

Statistical treatment of time series data

Although there was a regular biweekly sampling scheme for pelagic observations, sampling was not always carried out in exactly 2-week intervals over the 28-year study period. Therefore, available data of all parameters over the whole study period were linearly interpolated at daily resolution ([Livingstone, 2003](#); [Sapna et al., 2015](#)) and were averaged afterwards over a 2-week period. These biweekly interpolated data are used throughout this study with the only exception of retrieving k_{PAR} from z_{Secchi} (see

[Supplementary Material_2](#)). This interpolated data set avoids biases in data presentation due to a more frequent sampling of a measurement campaign during the reference year 1987 and years of particular interest of restoration progress as well as a generally lower sampling frequency in late autumn and winter compared with spring and summer ([Teubner et al., 2018a](#); [Teubner et al., 2018b](#); [Teubner et al., 2020](#)).

Results

Alte Donau oxbow lake map and macrophyte cover

The elongated shape of lake morphometry of the former main stretch of the Danube River, the oxbow lake Alte Donau, is shown in [Figures 1A–C](#). Year 1987, the reference year ([Figure 1A](#), middle panel), gives evidence that the shallowness of the water body suits well for building up dense meadows of underwater vegetation. Recovering from the hypertrophic state, macrophyte resettlement started at shallow littoral shore sites as depicted for 2001 in [Figure 1A](#) (right panel).

Basic pelagic-benthic parameters of trophic situation and underwater light

Time series data, which start with the mesotrophic reference year 1987, progress until to the 2 years of hypertrophic state in 1993 and 1994 and further subsequent lake treatment years up to 2019, are displayed for the pelagic trophic state and macrophyte development together with various facets of water transparency in [Figure 3](#). The long-term development of concentrations of Chl-a and TP are associated to each other ([Figures 3A,B](#)). Annual maxima in summer, which are most clearly seen for Chl-a for the period 1993–2003 and for TP for the whole observation period, coincide with the summer maxima of SWT shown in [Figure 3C](#). After chemical phosphate precipitation and successive macrophyte re-settlement (stage 2 and 3 of lake restoration treatment), the concentrations of both TP and Chl-a fell to low levels in 2004, with a simultaneous increase in z_{Secchi} to about 3–4 m ([Figures 3A,B](#)). Furthermore, a noticeable macrophyte biomass was measured in 2003 and became even higher in 2004 for the first time after the reference year 1987 ([Figure 3E](#)). The percentage of surface ambient light at mean lake depth ($I_{Z_{mean\ depth}}$) increased at all three sites of the major impoundments (AD1, AD3 and AD4) to about 10%–30% in 2003 and to 20–70% in 2004 ([Figure 3B](#)). For the period 1993–2003, i.e., covering stages from nutrient-rich to still moderate Chl-a and TP concentrations, a clear seasonal pattern of light availability was observed for depth values of z_{eu} , $z_{macrophytes}$ and $z_{optimum}$ ([Figure 3D](#)), which were

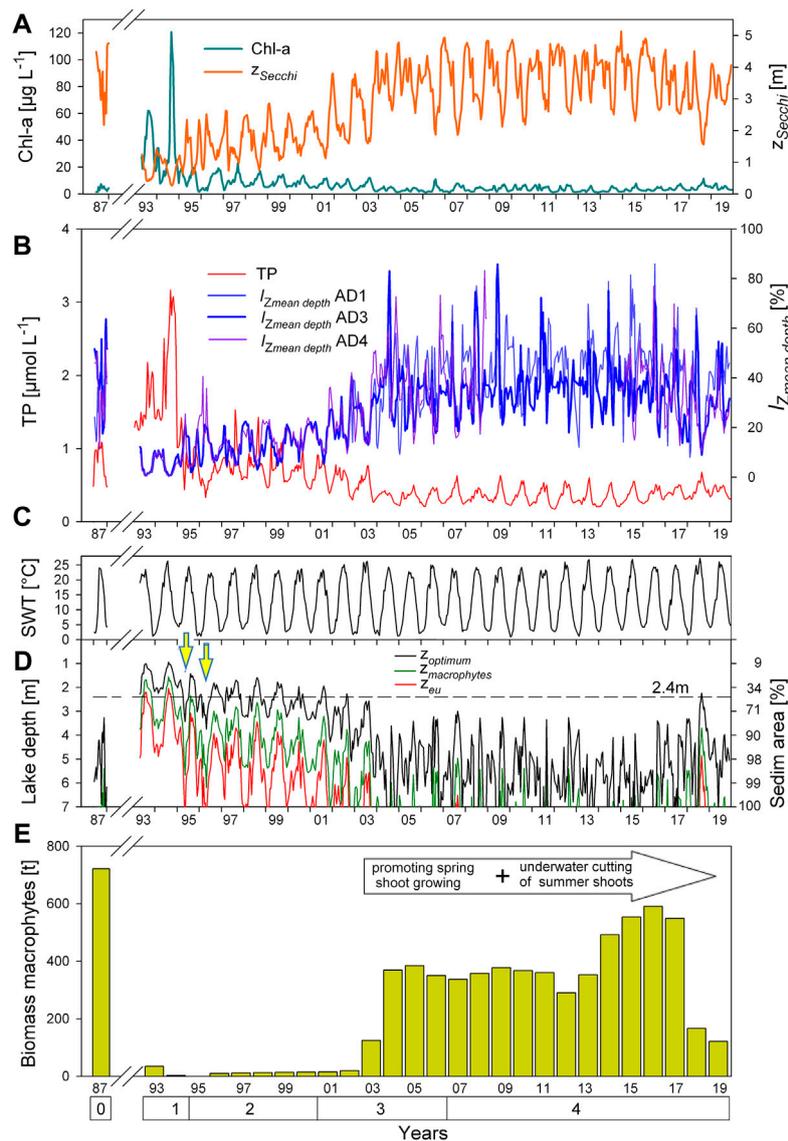


FIGURE 3

Time series of pelagic-benthic settings characterizing the macrophyte dominated, mesotrophic reference conditions in 1987 (stage 0), the hypertrophic algal turbidity (stage 1), the restoration with chemical phosphate precipitation treatment (stage 2), the re-settlement of macrophytes (stage 3) and the sustained recovery (stage 4). **(A–B)** Seasonal development of drivers of pelagic turbidity, i.e., planktonic algae (indicated by Chl-a concentration per L) and total phosphorus (TP concentration per L) compared with the seasonality of water transparency measured by z_{Secchi} , and by the percentage of surface ambient light at mean depth ($I_{z_{\text{mean depth}}}$) at the three main sampling sites. **(C)** Surface water temperature (SWT) graphically illustrates the seasonal progression during the 28 years of measurement. **(D)** Depth of light penetration satisfying minimum light requirements, i.e., at 1% for planktonic algae (z_{eu}) and at 3% for macrophytes ($z_{\text{macrophytes}}$), and depth of optimum growth of primary producers at 12% surface ambient light (z_{optimum}) of each sampling date, and the corresponding lake sediment area (%; depth resolution = 0.10 m) exposed to 12% surface ambient light. The dashed line indicates the mean lake depth, the arrows mark the 2 years of chemical phosphate precipitation. **(E)** Annual yield of macrophyte biomass as DW of the whole lake; the arrow indicates the beginning of intensive macrophyte management measures by short-term lowering of the vernal water level and summer mowing (see methods). Time series shows biweekly data in A–D and annual data in E. With exception of $I_{z_{\text{mean depth}}}$, A–D are averages over the three main sampling sites.

calculated from the mean k_{PAR} over the three sampling sites AD1, AD3 and AD4. The depth for minimum light requirement of phytoplankton (z_{eu}) coincides with the mean lake depth of 2.4 m ($z_{\text{mean depth}}$) or with even slightly

deeper water layers during already algal-turbid nutrient conditions in 1993/1994. A further increase in z_{eu} immediately followed the chemical phosphate precipitation and the consequently reduced Chl-a in 1995 and 1996. The z_{eu}

in winter already reached the maximum lake depth of 7 m and in summer a depth of 4–5.5 m. Furthermore, about 70–90% of the sediment area at the lake bottom was exposed to at least 1% of surface ambient light in 1995/1996. Results regarding the exposure to minimum light requirement of 3% surface ambient light for macrophytes ($z_{macrophytes}$) were close to those of z_{eu} . According to Figure 3, both z_{eu} and $z_{macrophytes}$ rapidly exceeded $z_{mean.depth}$ by far with decreasing TP and Chl-a year by year and subsequent restoration measures (until 2002), thus providing 1% and 3% light exposure to more than 70 or 90% of the sediment area, respectively. This development, however, was not accompanied by an immediate step-by-step increase of the macrophyte yield (Figure 3E).

A different picture comes up when assessing the exposure depth to 12% surface ambient light, $z_{optimum}$. In hypertrophic years 1993/1994, $z_{optimum}$ was always shallower than $z_{mean.depth}$. During years of phosphate precipitation and the following years focusing on re-establishment of macrophytes (1995–2001), $z_{optimum}$ was found at about 5.5 m in winter, and at the shallow depth of about 2 m in summer. In 2003, $z_{optimum}$ went beyond $z_{mean.depth}$ in summer for the first time, with an exposure to 12% surface ambient light for more than half of the total sediment area at the lake bottom. Looking at the development of macrophyte yield in Figure 3E, year 2003 is found to be the first year of remarkable macrophyte development, yielding 125 tons DW biomass. The year 2003 is a transition year from a period of a stagnant sparse macrophyte formation of less than 20 tons annual biomass (DW) from 1993 to 2002, to a period of a plateau of annual biomass development of 350 tons from 2004 to 2013. A further increase in macrophyte biomass occurred between 2014 and 2017, with a maximum value of almost 590 tons DW, which corresponds to about 82% of the biomass of the reference year 1987. Finally, macrophyte biomass declined in 2018 and 2019. Over the long period from 2004 to 2017, Chl-a and TP appear to be stabilized around a low concentration level with only a small increase in 2018/2019 (Figures 3A,D), while underwater light availability slightly decreased, as e.g., determined by lowered values for z_{Secchi} and $z_{optimum}$ (Figures 3A,B,D).

Optimum light exposure on the pelagic and benthic habitat

Empirical time series data over 28 years thus show that year-to-year progression of macrophyte yield is linked to an achievement of optimum light requirements, $z_{optimum}$, rather than the achievement of the minimum light requirements such as z_{eu} and $z_{macrophytes}$. These results raise the question how the water volume that is receiving at least 12% surface ambient light (% photic_{>12%} pelagic habitat) is changing over time when compared to the size of the sediment surface exposed

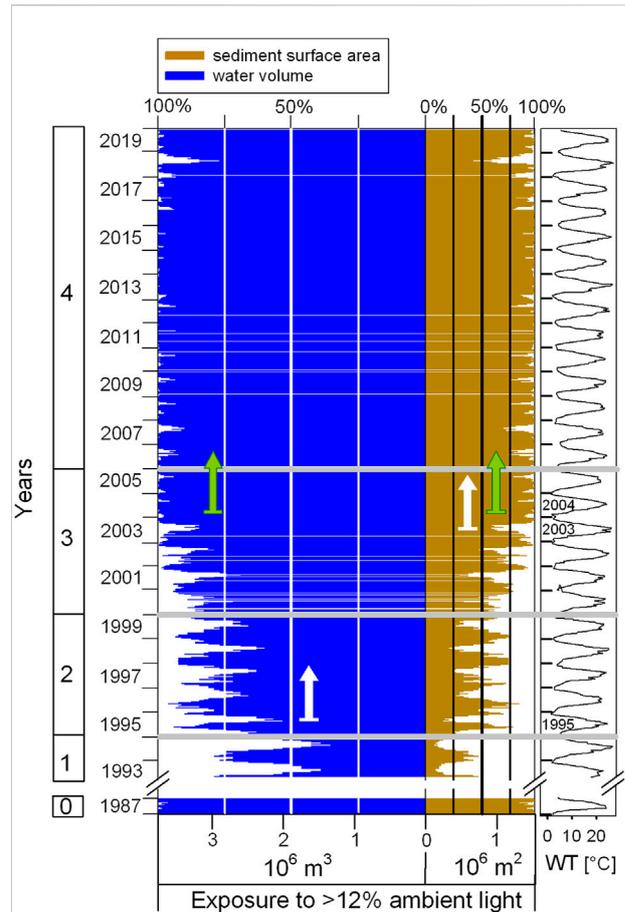
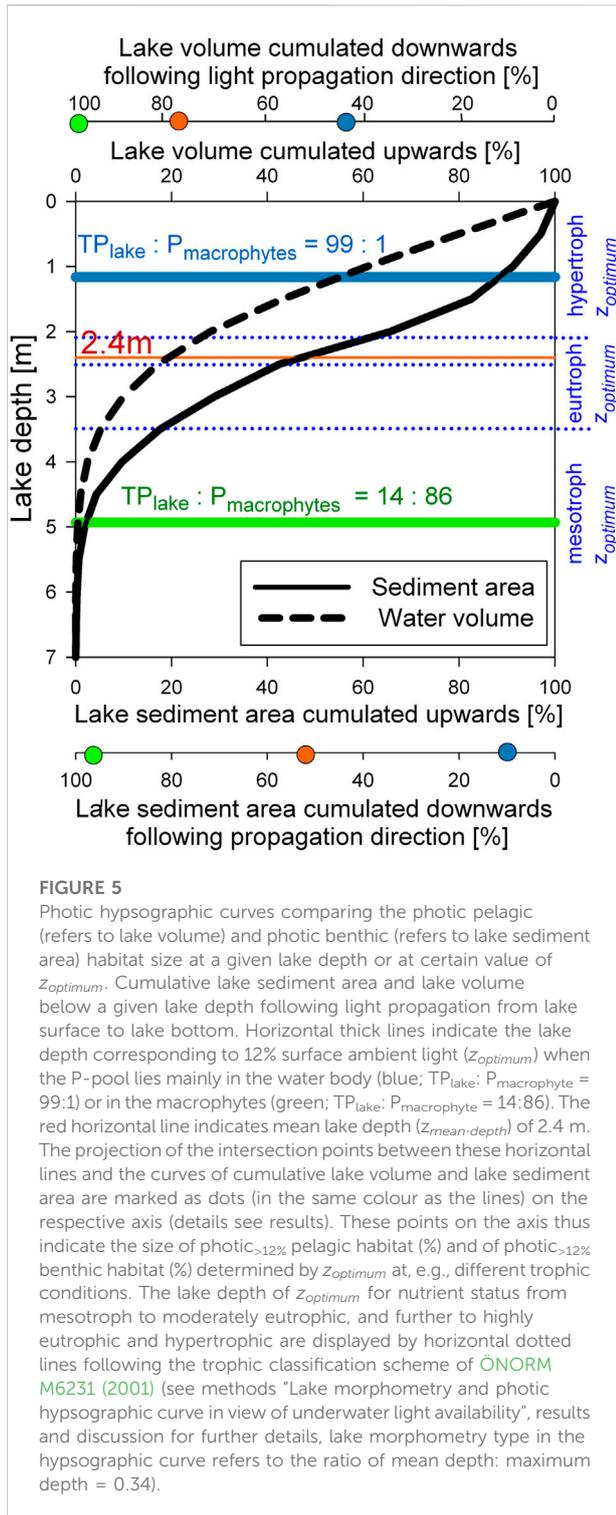


FIGURE 4

Time series of exposure to optimum light on the pelagic (water volume, % photic pelagic_{>12%} habitat size) and benthic habitat (sediment surface area, % photic benthic_{>12%} habitat size) during lake restoration. White arrows indicate the first year since the beginning of lake restoration measures when at least 50% of total water volume (1995) and of total sediment area (2003), respectively, were exposed to at least 12% surface ambient light during growing season. Green arrows mark optimum light conditions throughout the whole water body (almost 100% lake volume) and the whole lake bottom (almost 100% lake sediment area), reached in 2004. WT graphically illustrates the seasonal progression during 28 years of measurement, thick grey lines the stages of lake restoration measures as in Figure 3. All time series data are averages over the three main sampling sites, shown in biweekly intervals. See also Figure 5 for further details.

to at least 12% surface ambient light (% photic_{>12%} benthic habitat).

Figure 4 shows the change over time for the % photic_{>12%} pelagic habitat and % photic_{>12%} benthic habitat (lake bottom) during the 28-year study. In the reference year 1987, almost 100% of both, water volume and sediment surface area, were exposed to 12% surface ambient light. Highest algal turbidity in 1993/1994 stands for far less than half of the lake water volume (<< 50%) and far less than a quarter of the lake sediment surface area (<< 25%) that is being exposed to optimal light



availability during summer. With the beginning of the lake restoration, i.e., during the first year of phosphate precipitation in 1995, already more than half of the water volume in summer was exposed to at least 12% surface ambient light. In summer of 2003, i.e., with a delay of 8 years,

the same light exposure exceeded half of the sediment surface area (see white arrows in Figure 4, see above description for Figure 3 with regard to 2003 being a transition year). In summer 2004, at least three quarters (>75%) of both the lake volume and the sediment surface area were exposed to 12% surface ambient light (green arrows in Figure 4). After 13 years of stable light availability during summertime with almost 100% for both the pelagic and the benthic habitat (2005–2017), light availability shortly decreased again in midsummer 2018 (see seasonality patterns based on WT). Already less than half of the sediment surface area but still slightly more than three quarters of the water body were exposed to optimum light intensity during this year.

Photic hypsographic curve

Over the years of lake restoration, the time shift between lake water (photic_{>12%} pelagic habitat) and lake bottom surface light exposure (photic_{>12%} benthic habitat) is due to the characteristic of lake morphometry of this shallow oxbow lake, as illustrated by the photic hypsographic curve (Figure 5). The cumulative lake water volume above a given lake depth is a convex curve, while those for the cumulative lake sediment surface area is a slightly concave curve. Following the direction of incident sun light, lake volume and lake underwater sediment area are cumulated from the top of the lake to the lake bottom in this photic hypsographic curve. With the spatial coincidence of $Z_{optimum}$ and $Z_{mean-depth}$, already the largest portion of total lake volume (80% photic_{>12%} pelagic habitat), but only about half of the total sediment area (53% photic_{>12%} benthic habitat) are exposed to at least 12% surface ambient light (see orange projection points in Figure 5). In addition, considering the potential of habitat size with optimal light availability of primary producers, the advantage of the pelagic habitat (phytoplankton) increases over the benthic habitat as the lake becomes more nutrient rich (see categories of trophic classification from meso- to hypertrophic in Figure 5). With different trophic states, the proportion of phosphorus bound in the pelagic pool (TP_{lake}) and by macrophytes ($P_{macrophytes}$) changes. When phosphorus is mainly allocated to the pelagic habitat, e.g., as measured with $TP_{lake} : P_{macrophytes} = 99:1$ in 1994, $Z_{optimum}$ is 1.2 m in summer and thus very low. With this shallow layer of 1.2 m, however, already 57% of the lake water volume but only 17% of the lake sediment surface area are exposed to at least 12% surface ambient light, supporting primary production and associated processes of the pelagic habitat at the expense of the benthic habitat (see blue projection points in Figure 5). In turn, when P is mainly allocated to the macrophyte standing crop, e.g., as measured for the mesotrophic reference year 1987 with $TP_{lake} : P_{macrophytes} = 14:86$ and summer $Z_{optimum} = 4.9$ m, the exposure to at least 12% surface ambient light reaches

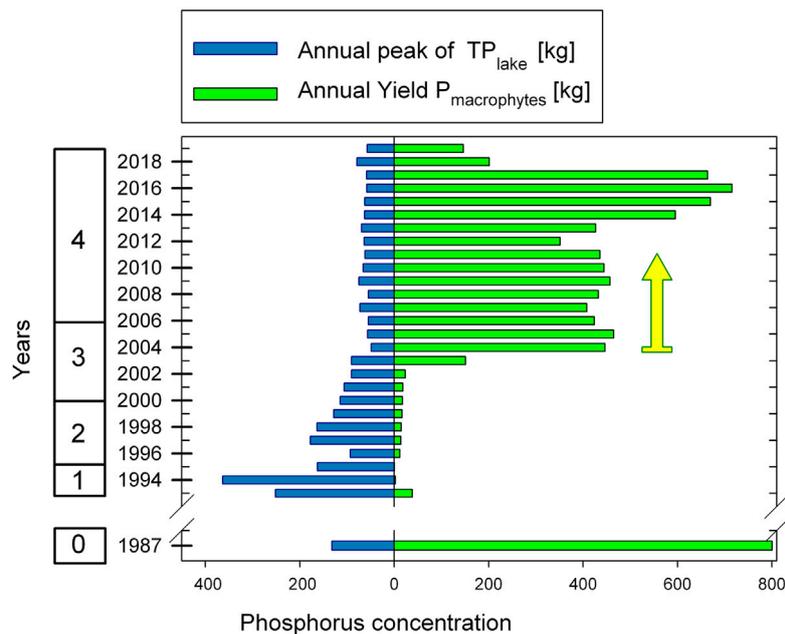


FIGURE 6

Time-series of the phosphorus storage pool built up by submerged macrophytes. Annual yield of P bounded in macrophytes ($P_{\text{macrophytes}}$) compared with annual peak of lake TP (TP_{lake}). The arrow points to the year 2004, when $P_{\text{macrophytes}}$ concentrations exceeded the annual peak concentration of TP_{lake} by one order of magnitude during the re-settlement of macrophytes.

99.5% of the pelagic habitat and 97.7% of the benthic habitat. Therefore, the mesotrophic nutrient status provides the same potential for photic colonization for both habitat types if assessed by underwater light availability (see green projection points in Figure 5).

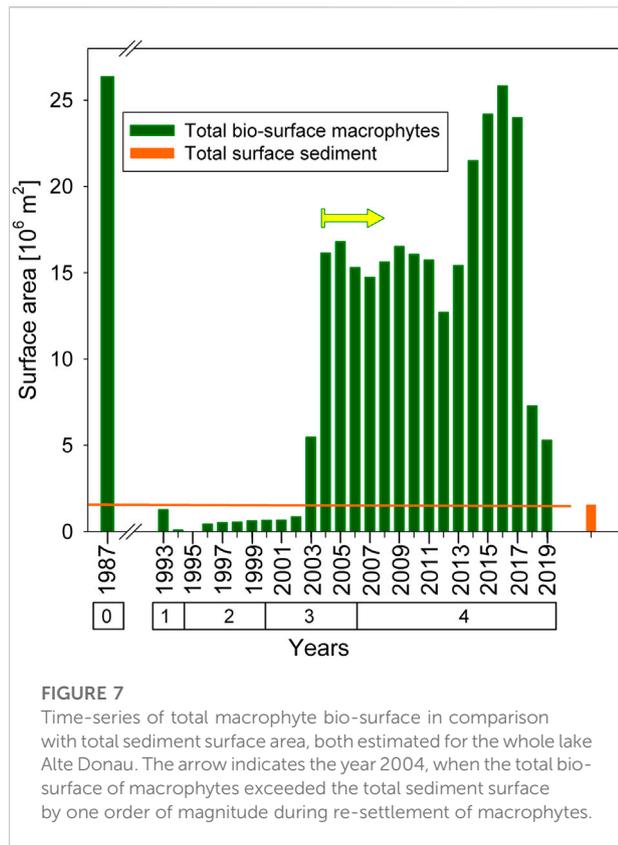
Phosphorus storage pool built up by submerged macrophytes

The time series for TP_{lake} (annual peak concentration per lake volume) and $P_{\text{macrophytes}}$ (P bound by macrophytes calculated from annual biomass yield, see also methods) is shown in Figure 6. During the algal turbid hypertrophic state in 1993/1994, elevated TP_{lake} values correspond to low or zero $P_{\text{macrophytes}}$. After the chemical phosphate precipitation treatment in 1995/1996, values of TP_{lake} slight recovery afterwards before further steadily decreasing until 2002. $P_{\text{macrophytes}}$, however, remained stable at a low level over these 6 years. In 2003, identified as transition year by macrophyte yield (see results for Figure 3), $P_{\text{macrophytes}}$ significantly increased for the first time during the whole restoration period and was about twice as high as TP_{lake} . In the following year, 2004, $P_{\text{macrophytes}}$ increased at the expense of TP_{lake} as the pelagic summer peak became particular low. The role of macrophytes as a phosphorus storage pool became quantitatively relevant for the ecosystem in 2004, as $P_{\text{macrophytes}}$ values were exceeding TP_{lake} by

about one order of magnitude (2004: $P_{\text{macrophytes}}$ is 9.2 times higher than TP_{lake}). This storage capacity was maintained the following years until 2017. The highest storage capacity by $P_{\text{macrophytes}}$ relative to TP_{lake} was outlined during in the period 2015–2017, when $P_{\text{macrophytes}}$ was higher than TP_{lake} by a factor between 10.8 and 12.3. The last 2 years of investigation, characterized by a decline of macrophyte yield (see methods), referred to a situation like in 2004 when $P_{\text{macrophytes}}$ was about twice as large as TP_{lake} alone.

Lake macrophyte bio-surface in comparison with lake sediment surface area

Beside the role of macrophytes as P-storage pool, macrophytes are provisioning an additional habitat through their bio-surface. Figure 7 A shows the annual bio-surface of macrophytes in comparison with the size of the total sediment surface area. The highest bio-surface is estimated for the reference-year 1987, during which the underwater meadow was mainly comprised of charophytes. With eutrophication and beginning of restoration, until 2002, macrophyte formation and, accordingly, the macrophyte bio-surface was less than the surface area provided by the sediment of the whole lake bottom. In year 2003, for the first time since the beginning of the restoration, the bio-surface exceeded the



surface area of the sediment by a factor of 3.6. In 2004 and following years until 2013 the excess reached one order of magnitude. In the following 4-year period (2014–2017), highest bio-surface of macrophyte assemblage dominated by *M. spicatum* exceeded the sediment surface area of the whole lake bottom by a factor of 16.8, which was in the same range as the bio-surface during mesotrophic conditions, when macrophyte meadows were mainly build up by charophytes.

Discussion

At a first glance, macrophytes do not seem to be in a top position when referring to the superiority between the two main light utilizing domains, as the planktonic algae near the lake surface are spatially much closer to the source of incident light than bottom dwelling macrophytes. However, this changes when macrophytes can grow successfully (Jeppesen et al., 2012). In fact, macrophytes play an important role for a shallow lake ecosystem if large standing crop can be achieved.

Many publications estimate macrophyte yield by biomass (Bergahn et al., 2007; Exler and Janauer, 2012; Pall, 2018) or

macrophyte coverage (Ibelings et al., 2007; Cheruvilil and Soranno, 2008; Dembowska et al., 2018; Ferreira et al., 2018), but the magnitude beyond the stated yield is often not shown. Addressing the phosphorus storage capacity by macrophyte tissue underpins the ecological-biochemistry role of macrophyte yield, which is most relevant for lake restoration to sustain TP at a low concentration level in the lake (Granéli and Solander, 1988; Clarke, 2002; Kufel and Kufel, 2002; Søndergaard et al., 2002; Hupfer and Dollan, 2003; Honti et al., 2020). Capturing the role of bio-surface for provisioning an additional habitat structure would refer to the spatial context of macrophyte yield. The latter contributes to the debate whether recourses or habitats are primarily controlling an ecosystem (Craig et al., 2015). Mature macrophyte stands are thus of great importance for providing ecosystem services in many ways (e.g., Nöges et al., 2010; Jeppesen et al., 2012; Thomaz, 2021).

Retrieving underwater light availability from z_{Secchi} for assessing underwater light climate for macrophyte growth

The perspective of z_{Secchi} changed over three epochs (Teubner et al., 2021), i.e., 1) from a measure of physico-optical property estimating underwater distances, 2) to a biological perspective as indicator for lake eutrophication (e.g., Vollenweider, 1968), and 3) to a target parameter of overall success of sustained lake restoration and ecosystem services (e.g., Teubner et al., 2020). Using z_{Secchi} as a proxy for estimating water quality or for z_{eu} is therefore common in limnology (e.g., Ibelings et al., 2007; Znachor et al., 2018; Chang et al., 2020; Teubner et al., 2020; Dubey et al., 2021). Retrieving ambient light availability for primary producers from z_{Secchi} , however, as exemplified in the present study, is complex. The annual loop pattern, when plotting Chl-a, DOC and z_{Secchi} in relation to k_{PAR} in the present study, stands for a gradual seasonal change of interlinked optical properties of the lake water (aspects of seasonal size and species shift among phytoplankton, see Teubner, 2000; Padisák et al., 2009; for DOC of allochthonous sources, see Reitsema et al., 2018; Doyle et al., 2019, for autochthonous DOC release by algal plankton see Larsson and Hagström, 1979; Bjørrisen, 1988, and by macrophytes Ali et al., 2019; Reitsema et al., 2018, 2021; Wolters et al., 2019; Somogyi et al., 2022) (details see Supplementary Material S2). It thus well illustrates that retrieving k_{PAR} and associated optical parameters from z_{Secchi} cannot be broken down to one certain lake situation but needs to take into consideration the change over time within seasons and—as many physical and biotic parameters can tend to change over years—also at larger time scales (e.g., Paul, 1989).

The relevance of lake morphometry for the size of photic_{>12%} pelagic and photic_{>12%} benthic habitat

With an increase of the water transparency as the major target of lake restoration (Chorus et al., 2020; Teubner et al., 2020), light availability increases not only in the pelagic habitat but also in the benthic habitat, where it initializes macrophyte growth on sediment surface (Istvánovics et al., 2008; Pall, 2018; Dubey et al., 2021). The emergence of macrophytes raises the question to what extent in time and space an improvement of water transparency is reflected by an increase of photic_{>12%} pelagic habitat size (% of total water volume) on the one side and by an increase of photic_{>12%} benthic habitat size (% of total sediment surface area) on the other. Most studies, however, focus just on one of the two habitats. Concerning the photic control of either the pelagic or the benthic habitat often takes advantage of z_{Secchi} or z_{eu} in field studies (pelagic habitat, e.g., Chen et al., 2003; Tolotti and Thies, 2002; Chorus et al., 2020; benthic habitat, e.g., Søndergaard et al., 2013; Baart et al., 2010; Dubey et al., 2021; Gao et al., 2020). In our study, however, we were able to show that the increase in the percentage of photic_{>12%} pelagic habitat was not consistent with a concomitant increase in the percentage of photic_{>12%} benthic habitat. The fact that at the beginning of a lake restoration the relative increase (%) of the photic_{>12%} benthic habitat could not keep pace with the rapid increase (%) of the photic_{>12%} pelagic habitat is not a question of just a time-shift, but an effect of deficiency or lagging behind, which is determined by the specific lake basin morphometry as shown in our case for Alte Donau. The time-space pattern revealed that after the beginning of lake restoration in 1995, the pelagic habitat immediately underwent an increase of photic_{>12%} conditions to 50% of the pelagic habitat size, and thus responded to a sudden increase of water transparency. However, the achievement of optimum light requirement for half of the sediment area required further 8 years. After just another year of improvement in water quality, both habitats, i.e., the water body and the sediment, reached at least 75% of photic_{>12%} conditions in summer. According to the shallow lake basin, the discrepancy between the size of photic_{>12%} pelagic and photic_{>12%} benthic habitat is the highest when water transparency is lowest, as illustrated by the photic hypsographic curve for hypertrophic conditions in Alte Donau. This might be relevant for other shallow lakes with similar lake basin morphometry and trophy. It stands for the predominance of pelagic algal growth under nutrient rich conditions and confirms the hysteresis theory of alternative stable states in shallow lakes (Scheffer et al., 1993; Ibelings et al., 2007; Jeppesen et al., 2012; Dokulil et al., 2018a). The better the water quality, which means the more ambient photosynthetic light becomes available in deeper strata near the lake bottom, the lower the discrepancy of light exposure between benthic and pelagic habitat until maximum photic_{>12%} conditions (100%) for the whole lake water volume and the whole lake bottom surface area

are finally reached. In other words, the closer the increase for the percentage of photic pelagic_{>12%} and photic benthic_{>12%} habitat size is, the less the planktonic algal and cyanobacterial organisms can take advantage over the respective benthic photosynthetic organisms, determined by lake morphometry (and as illustrated by the photic hypsographic curve). But the time span that is required to overcome this light exposure discrepancy between pelagic and sediment habitat depends on the efficiency of restoration measures and thus relates to lake management in the long-term. Not only for Alte Donau, but also for other studies about the restoration of hypertrophic shallow lakes, the achievement of sustainable lake restoration is often hampered for years (Ibelings et al., 2007; Chorus et al., 2020; Honti et al., 2020).

While in this study we primarily looked on how restoration effort by increasing water transparency succeeded, we now discuss how vulnerable the ecosystem can be in view of deterioration associated with ongoing lowering of water clarity. As exemplified for Alte Donau, during the last 3 years of decreased macrophyte yield (see intense mowing in the methods), the size of the photic_{>12%} benthic habitat became markedly smaller but was not responded by a remarkable concentration increase of TP_{lake}. According to the finding by the photic hypsographic curve for Alte Donau, the slower a restoration progresses to overcome the delay of an enlargement photic_{>12%} benthic habitat, the faster the turn back might be, as the photic_{>12%} benthic habitat is primarily affected by this. Such an accelerated deterioration of a shallow lake might indeed succeed if submerged vegetation is only sparsely developed. A sudden turn back to an algal turbid lake, however, is not observed in case of well-established underwater vegetation meadows. Such a situation is described for 1987 in Alte Donau, by an already present process of slow macrophyte loss during late mesotrophic state (see method). The advance of the photic_{>12%} pelagic at the expense of photic_{>12%} benthic habitat with ongoing deterioration of water quality and, i.e., an increase of pelagic algal turbidity, might thus largely depend on the extent of the standing crop of macrophytes. In case macrophyte stands are already established in such a situation, tall growing species including phytal photosynthetic microbiota might still have access to sufficient incident light. For both, macrophyte meadows and phytoplankton, photosynthetic organisms are known to have a high capacity for succeeding well under different light conditions. Greisberger and Teubner (2007) have exemplified the wide range of pigment adjustment of phytoplankton to ambient light conditions changing over seasons. Macrophytes such as charophytes, for example, are also known to adjust to a large range of light conditions within a certain range. Some are even known for their dim-light requirement most relevant to survive at deeper water layers (Schagerl and Pichler, 2000; Zhang et al., 2018). As submerged macrophytes built up their own thalli or shoot architecture, they thus do not necessarily suffer from light limitation in deep bottom layers, but take advantage of having

grown towards the lake surface as survival strategy which would delay the death of aquatic vascular plants or charophytes and thus also buffer short-term deterioration in water quality. This is in agreement with the finding that established macrophyte stands contribute to stabilize a lake system (Scheffer et al., 1993; Jeppesen et al., 2012). A further decrease of water transparency due to an ongoing eutrophication scenario, however, would finally favour again an accelerated overshooting growth of light harvesting pelagic organisms at the expense of macrophytes determined by photic hypsographic conditions mentioned before. The remaining photic_{>12%} benthic habitat would then become dramatically smaller in size over time and $z_{optimum}$ would turn to an increasingly shallow layer close to the top lake surface.

Underwater light climate: The achievement of optimum rather than minimum light requirement plays a role

In general, plants respond not only to quality and quantity of light by an adjustment of their pigment composition to accomplish growth and thus biomass yield. Light is also ecologically important at the level of light signal perception (Smith, 2000). The water level draw-down of about 25 cm for only few days in spring (see method), might be perceived as light signal triggering vernal development by seed germination, leaf expansion and shoot development of submerged macrophytes even in slightly deeper layers of the littoral zone (Dokulil M. T. et al., 2018; Pall, 2018; Pall and Goldschmid, 2018; Teubner et al., 2020). According to Pall (2018), it is seen as an important restoration measure for the successful re-establishment of macrophytes as short-term vernal water level draw-down from 2002 onwards was concomitant with an increase in macrophyte yield in Alte Donau. With the present study, we still see the importance of vernal water draw-down. Nevertheless, to accomplish large macrophyte yields, the availability of sufficient light during the main growing season might be of particular importance. In this point we go further than in the previous study (Teubner et al., 2020), where an emphasis was put on z_{eu} and $z_{macrophytes}$ in addition to optimum light conditions. In the present study, we identified that an improvement of water transparency for macrophyte establishment must refer to $z_{optimum}$ as macrophyte yield followed the achievement of optimum light requirement at lake bottom—not of those of any of the both minimum requirement (z_{eu} , $z_{macrophytes}$) mentioned before. When half of the total sediment surface was exposed to 12% surface ambient light during the growing season (in winter, the water transparency is usually even higher), the significant macrophyte development started (year

2003). Thus, we can state that passing the ecological threshold of 50% photic_{>12%} benthic habitat, a sustained growth of macrophytes can be assumed in this shallow oxbow lake. One year later, with further increase of water transparency, macrophytes became the dominant photosynthetic domain, building up their overwhelming habitat architecture. Ecological thresholds, also called tipping points in applied aquatic sciences, are commonly discussed for lake assessment (e.g., Solheim et al., 2008; Vuorio et al., 2020).

The importance of macrophyte habitat structure beyond the biomass yield

With the significant increase of macrophyte yield due to lake restoration, about 50%–80% of the macrophyte biomass of the reference year was recovered. This macrophyte yield stands for a huge phosphorus storage pool, as $P_{macrophyte}$ exceeded TP_{lake} by about one order of magnitude. Furthermore, these macrophyte stands provisioned with their bio-surface an additional habitat which extended the size of the benthic habitat at lake bottom by even more than one order of magnitude.

Both the phosphorus content and the nutrient elemental stoichiometry of the aquatic plants vary among plant species or locations (e.g., Lukatelič et al., 1987; Mazej and Germ, 2008; Wang et al., 2018). Despite this rather narrow range of variation for phosphorus acquisition among plant species, the essential role of macrophytes for lake ecosystems lies in their phosphorus storage capacity, which means retaining this nutrient element and thus making a large amount of phosphorus not bio-available for the development of photosynthetic plankton micro-organisms during the growing season of a current year. In view of an overwhelming phosphorus pool retained in macrophyte stands under sustained low TP concentration (Lukatelič et al., 1987), we primarily see macrophytes as a significant sink for phosphorus in Alte Donau. This interpretation is in agreement with other studies claiming that macrophyte stands can be considered as permanent or at least temporary phosphorus sink and hamper a fast phosphorus turnover in the lake (Granéli and Solander, 1988; Donk et al., 1993; Clarke, 2002; Kufel and Kufel, 2002; Søndergaard et al., 2002; Hupfer and Dollan, 2003; Honti et al., 2020). An overwintering of macrophytes in Alte Donau in recent mild winters (K. Pall, personal communication) extends their storage capacity even beyond the growing season (other lakes: e.g., Jeppesen et al., 2020; Brzozowski and Pelechaty, 2022). The plankton community is in principle also known to act as a sink for phosphorus if grown under phosphorus deficiency, i.e., after phosphate precipitation treatment in Alte Donau (Teubner et al., 2003); but when compared with the huge storage pool of mature macrophyte stands it appears less relevant in terms of its quantity.

Macrophyte and phytoplankton phosphorus acquisition

Discussing the ecological role of macrophytes and phytoplankton as a phosphorus storage pool raises the question about the physiological background of phosphorus acquisition for both photosynthetic domains. Phosphorus is known to be the most limiting nutrient element in freshwaters (Vollenweider, 1968; Schindler, 1977; Moss et al., 2013). An acquisition by luxury phosphate consumption building up huge cell-internal phosphate storage pools (polyphosphates) on the one hand, and a bio-active uptake system which allows to utilize ephemeral nano-scale phosphate patches efficiently (e.g., Falkner et al., 1989) on the other hand, roughly describe the wide scenarios of sophisticated phosphate incorporation by photosynthetic organisms. Phosphorus uptake often relies on a cascade of high and low affinity uptake systems (Epstein, 1972) depending on the supply and degree of starvation of organisms. Many phytoplankton species can thus cope well with an environment of either low or high phosphate supply (e.g., Istvánovics, 2008), which is also the case for many vascular plants (Raghothama, 1999). The growth inhibition of charophytes by “toxic” maximum phosphorus concentrations (Forsberg, 1964), might be again not out of the rule among primary producers since phytoplankton taxa in laboratory cultures also cannot survive after excessive phosphorus uptake (for cyanobacteria: K. Teubner, personal communication; green algae: Li et al., 2018).

The utmost phosphorus acquisition for seasonal development of underwater vegetation coincides with that of the phytoplankton, in particular if the vegetative parts of macrophytes grow periodically in the water (Reitsema et al., 2021). The demand of phosphorus for macrophyte growth is highest in spring (Vymazal, 2007). This agrees with Alte Donau (Pall, 2018), where the net change rate of macrophyte biomass increase was highest during the beginning of the growing season (04.05.-26.05.2000), coincident with the vernal phytoplankton increase with peaking net change rate in the second half of May 2000 (calculated from Teubner et al., 2018a). Also, global warming, which has been shown to have an impact on Alte Donau (Teubner et al., 2018b; Teubner et al., 2020), might affect the phenology of both plankton and macrophytes through time-shifts of vernal leaf-out and overwintering or relative growth rate, as also reported from other lakes (e.g., Zhang et al., 2015; Jeppesen et al., 2020; Brzozowski and Pelechaty, 2022). This all together might provide arguments that in principle both, macrophytes and phytoplankton, are closely related concerning the general rules and time pattern of phosphorus acquisition.

Concerning the benthic-pelagic coupling, we need to understand how lake phosphorus pools are utilized differently by macrophytes than by phytoplankton. Charophyte growth experiments of laboratory cultures (Zhang et al., 2018) and field bioassays (e.g., Forsberg, 1964; Siong and Asaeda, 2006)

did not answer the ecologically relevant question to what extent these algae by cells or by full habitus are incorporating bioavailable phosphorus sources from the pelagic habitat, while pelagic phosphorus is known to be important for growth of vascular submerged plants (Bristow and Whitcombe, 1971; Pelton et al., 1998) and planktonic algae (Dyhrman 2016). A large amount of pelagic phosphorus, however, is known to be bound by encrustation on macrophyte bio-surface (photosynthetically mediated calcite-phosphorus precipitation) mainly attributed to the charophytes (Kufel et al., 2013; Herbst et al., 2018; Sand-Jensen et al., 2018) in addition to some vascular macrophytes (e.g., Ostrofsky and Miller, 2017; for roots see Hupfer and Dollan, 2003). Despite a few exceptions (e.g., Schlegel et al., 2000), such bio-active encrustation is quantitatively rather negligible for algal plankton. In this view, the large bio-surface of healthy macrophyte stands in Alte Donau might be of advantage for bio-surface bounding or for cellular incorporation of pelagic phosphorus sources for building up dense underwater vegetation meadows as long as sufficient ambient underwater light is available and no other conditions occur that inhibit growth (e.g., by allelopathic effects, Gross, 2003). Box (1986) and Wüstenberg et al. (2011) furthermore verified that charophyte species in principle are able to utilize phosphorus efficiently by their rhizoids and thus can mobilize a certain amount of bio-available phosphorus from benthic habitat, as the vascular macrophytes commonly also do by their rhizomes (Bristow and Whitcombe, 1971; Melzer, 1999; Kleeberg, 2013; Zhang et al., 2019), but not phytoplankton organisms if strictly living in the pelagic zone. These studies thus argue that macrophyte-meadows, in particular if build up by charophytes, stabilize well low phosphate concentrations in lakes. It underpins the ecological importance of phosphorus allocation into the submerged macrophyte domain as most relevant for sustained lake restoration (Hilt et al., 2006; Kufel et al., 2013). The latter aspect indeed might have played an important role also in Alte Donau, as phosphorus binding capacity of the sediment was relatively high. The strongly calcareous sediment prevented P-release from sediment even under anoxic conditions (Ripl and Wolter, 1995; sediment characteristics in Supplementary Material S3).

Macrophytes providing additional habitat structure

Building up an additional habitat structure in a lake can be considered of utmost importance for the ecosystem rather than just providing biomass resources (Kuczyńska-Kippen and Nagengast, 2003; Craig et al., 2015). The spatial importance of the emergence of macrophytes is seen in the immensely large bio-surface area providing further living space for phytal organisms which goes beyond the size of the lake bottom area in Alte

Donau. The significance of the phytal habitat could be verified by a 28 times higher abundance of individuals for Chironomidae, followed by other MZB species, when compared with those in the lake sediment in Alte Donau (see [Supplementary Material S4](#)). This one order of magnitude higher phytal abundance underscores the vitality of such a habitat architecture of submerged macrophytes and agrees with other studies where submerged macrophytes allocated higher yields of MZB than compared with non-living substrate or littoral submerged shoots of *Phragmites australis* (e.g., [Feldmann and Nöges, 2007](#); [Yofukuji et al., 2021](#)). Nevertheless, densities of phytal MZB organisms can largely vary as micro-conditions of these specific environments are highly variable in space and time ([Cremona et al., 2008](#)), are superimposed by eutrophication (e.g., [Kahlert and Pettersson, 2002](#)), exposed to bio-chemical (allelopathic substances; [Gross, 2003](#)) or physical stress (flow-velocity in flood-plain systems; [Funk et al., 2013](#)) which finally may hamper development of attached living biota on aquatic submerged plants. Thinking about the suitability of macrophytes as microhabitat, might extend to the question of how attached organisms live. They aggregate in biofilms ([Battin et al., 2016](#)), and benefit from various photosynthetic nutrient sources delivered by the macrophyte host ([Ali et al., 2019](#); [Wolters et al., 2019](#)) or by attached living phytal algae and other microorganisms ([Dodds, 1991](#); [Wagner et al., 2017](#); [Rojo et al., 2020](#)). [Han et al. \(2018\)](#) describe in detail the ecologically most relevant benefit by such a specific “submerged macrophyte-biofilm system”. It underpins that the macrophytes might be seen as an ecological habitat entity for building up their own network for connecting food and energy exchange (see also [Zhang et al., 2016](#); [Wolters et al., 2019](#)).

Another important role of macrophyte habitat architecture for aquatic ecosystems is seen in the provisioning of food and shelter for spawning and nursery of vertebrates as discussed for fish in different studies ([Petr, 2000](#); [Meulenbroek et al., 2018](#); [Figueiredo et al., 2013](#); [Yofukuji et al., 2021](#); macrophytes themselves can be a significant food source for fish: [Yu et al., 2016](#); [Löffler, 1988](#); [Zhen et al., 2018](#)). Also for Alte Donau, [Waidbacher and Drexler \(2018\)](#) verified macrophytes and phytal biota as important food sources and macrophyte stands as valued niches for young fish. They claim that underwater macrophyte cutting for enhancing the recreational use of Alte Donau, can cause a dramatic damage to young fish (loss of one young fish per 2–2.5 kg of harvested FW macrophytes in 2005, 2006). The denser the macrophyte stands are, the more fish are expected to be harboured. The fish harboured from sparse to dense macrophyte stands increased on average from 2 to 30 individuals per “air-lift” catch (frame size = 2 × 2m) in Alte Donau ([Waidbacher and Drexler, 2018](#)). This increase of fish abundance by a factor of 15 underpins the ecological value in particular for a mature macrophyte habitat architecture and agrees with later fish surveys. According to [Gassner et al. \(2014\)](#), the abundance of fish in shallow zones of Alte Donau

in 2013 was twice as high as in other Austrian lakes with fish assemblages dominated by bleak (*Alburnus alburnus*) and confirms that fish take advantage from macrophytes in lakes (e.g., [Yu et al., 2016](#)). As long as water transparency suits well for cyprinid fish when searching for prey ([Wanzenböck and Schiemer, 1989](#); [Figueiredo et al., 2013](#)), the potential of food source provided by additional macrophyte habitat structure is undoubtedly important.

These few aspects about MZB and fish in Alte Donau verify again the ecological importance of macrophytes for building up a unique habitat architecture as a third main component in the network between the benthic (lake bottom) and pelagic (lake open water) living space.

Conclusion

In terms of implications for lake management derived from our study, we can state that focusing on optimum light conditions (12% surface ambient light, $z_{optimum}$) rather than on minimum light requirements (such as z_{eu} or $z_{macrophytes}$) might be more meaningful to follow the flourishing macrophyte development, which is particularly important when forcing the re-establishment of macrophytes. We further define the achievement of the photic_{>12%} benthic habitat conditions for more than half of the sediment surface area as the threshold for initializing the growth of remarkable macrophyte yield in shallow lakes. According to this result, passing this ecological threshold serves as an important step in the sustained restoration of a hypertrophic lake, i.e., is an indicator of significant progress of lake treatment.

According to our study, a delay in the light exposure of the lake bottom area compared to the lake water volume is implicitly related to lake basin morphometry (identified by photic hypsographic curve) and might thus differ among lakes. Only the time span (number of years) that is required to overcome this delay depends on the efficiency of restoration measures and thus relates to a sustained lake treatment in the long-term.

On the one side, mature macrophyte stands have a huge storage capacity of phosphorus (macrophyte tissue) being one order of magnitude higher than peak concentrations of TP of the whole lake water body. On the other side, mature macrophyte stands provide a huge structural bio-surface that is one order of magnitude larger in size than the whole lake sediment area, and thus can harbour an enhanced number of further freshwater biota. Hence, according to our study, massive stands of macrophytes can be seen as a significant sink for phosphorus in the ecological-biochemical context and can also be understood to provision an immensely large bio-surface of additional living space in the spatial context. Our results therefore support the finding that a mature vital macrophyte habitat architecture can indeed serve as an important structural element linked to the

benthic and pelagic habitat in a lake. We thus conclude, that the emergence of massive vital architecture built by submerged macrophytes, which is most important for the sustainability of water quality and for providing ecosystem services, goes far beyond being understood as being part of the benthic habitat. According to our main findings, submerged macrophytes might be rather seen as a third important unique habitat in addition to the benthic and pelagic habitat in shallow lakes.

Data availability statement

The datasets generated for this study are available on request to the corresponding author.

Author contributions

KT mainly conceived the manuscript idea, data analysis, preparation of graphs and text. IT conducted advanced data processing concerning underwater light attenuation and photic habitat sizes, writing and critical reading at all stages of ms preparation. MT contributed to the main idea and writing about ecological perspective, in particular of underwater light. KP contributed by providing raw data for the hypsographic curve and strong expertise in macrophyte biology and management, co-preparation of graphs, critical review of the ms. WK re-assessed measurements of underwater light. S-SD and HW contributed to fish relevant results, graphic preparation and writing of ms. MD contributed to methods of optical properties, sediment measures and restoration perspective Alte Donau, critical contribution at all stages of manuscript preparation and writing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

KP is CEO of the Systema GmbH.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2022.901924/full#supplementary-material>

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