Water level changes in Lake Constance and their relationship to changes in macrophyte settlement in the outflows of Lake Constance Upper and Lower Lake

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ARTICLE INFO

ABSTRACT

Since 2008, water level differences between Upper and Lower Lake Constance have increased after they decreased significantly in the 20th century. Questioning the causes leads to the hypothesis that the significant changes in the submerged macrophyte vegetation due to eutrophication and subsequent oligotrophication have played an essential role over the past decades. To clarify whether macrophyte vegetation is the cause of the changed water levels, the spatial distribution of Swiss pondweed *Potamogeton helveticus* (syn. *Stuckenia helvetica*) and the other submerged macrophytes was mapped in 2017. Swiss pondweed, in particular plays a key role as a perennial plant type in flow channels. Shoot densities and lengths of this species were recorded by diving. The investigations were supplemented by hydrodynamic modeling of the effects of macrophyte flow resistance on lake water level relationships.

The results show that *P. helveticus* has indeed increased significantly over the past decade. The species colonizes the bottom of flow channels in the Seerhein up to 6 m deep with up to 1000 shoots per square meter and a length of up to 5 m, whereas in the previous decades it only occurred at the edges of flow channels as small stands with shoot lengths of less than 1 m. In the shallow water zones outside the flow channels, stoneworts in particular have spread in the Seerhein over the past decade. The hydrodynamic modeling supports the hypothesis that aquatic plants are the cause of the changed lake water level conditions and illustrate the related changes in the flow velocity field.

1. Introduction

Since 2008, differences in water levels between Upper (Obersee) and Lower (Untersee) Lake Constance have gradually become larger (Fig. 1, BAFU, 2017; LUBW, 2017). Analysis of the water levels together with the outflows from Lake Constance to the upper Rhine show that the increase in water level differences does not result from lower lake floor levels, as would be expected due to erosion processes for example, but from differential changes in water levels of the two Lake Constance sub-basins for a given discharge rate. Thus the increase in water level differences seems to be the result of a hydrological change that has

raised water levels in the Upper Lake more than in the Lower Lake. Previous studies on Lake Constance water levels up to 2007 (LUBW, 2011) had shown that both the water levels and the water level differences in the two basins had dropped significantly over the past century. According to LUBW (2011), the linear trend of water level decrease from 1888 to 2007 is 20.9 cm/100 years in the Upper Lake and 9.3 cm/100 years in the Lower Lake. Water level differences between the two sub-basins had decreased by 11.6 cm/100 years over the same period. The time series recording the differences shows a particularly clear decrease from around 1950 to the end of the 1970s, although this nearly stagnated from the 1980s onwards. A sharp increase in the mean annual

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water level difference is particularly evident after 2007 (Fig. 1). The water level difference reached a maximum of 36 cm in 2017, compared to around 18 cm or less before 2008. Notable is the significant drop in the water level difference in 2019, by 7 cm to –t29 cm. The difference in water levels is higher in summer than in winter. In the period from 2010 to 2019, seasonal fluctuations averaged around 17 cm (Fig. 2).

A possible cause for the increasing water level differences is an accumulation of aquatic plants, particularly at the transition region between the Upper and Lower Lake (LUBW, 2017; BAFU, 2017). It is known that aquatic plants can cause congestion in flowing waters (Gils, 1962; Kahnt et al., 1989; Sand-Jensen et al., 1989; Sand-Jensen and Pedersen, 1999; Trepel et al., 2003; Bal et al., 2011). This is why regular mowing is carried out in many rivers to make the floodplains available for agriculture (Kahnt et al., 1989). Hydraulic resistance depends on the effective height of the vegetation, the shoot density and the species-specific growth characteristics (Wang and Wang, 2010).

The aquatic vegetation of Lake Constance has undergone dramatic changes in recent decades due to rapid eutrophication in the 1960s and 1970s and subsequent reoligotrophication (Lang, 1973, 1981; Schmieder, 1998; Dienst et al., 2012; Murphy et al., 2018). The rapid eutrophication process, which peaked at the end of the 1970s, was mainly induced by increasing phosphorous concentrations (Güde et al., 1998; Güde and Straile, 2016, p. 178; IGKB, 2018). A combination of investment in improved regional wastewater treatment plants and the "Regulations on Maximum Concentration of Phosphorous in Detergents and Washing Agents" act in Germany (Bundesministerium für Justiz und Verbraucherschutz, 1980) led to a gradual improvement in conditions by the 1990s, stabilizing at levels comparable to the 1950s (IGKB, 2018; Murphy et al., 2018).

Most aquatic plants largely die off in winter and then no longer contribute to congestion. However, the increasing congestion since 2008 is observed all year round. This implicates an evergreen macrophyte species as being responsible for the water level changes. One such evergreen species is Swiss pondweed (*Potamogeton helveticus*, syn. *Stuckenia helvetica*). This species only occurs in Lake Constance in the flowing areas of the draining channels between the Upper and Lower Lake and the outflow of the Lower Lake below Eschenz (Fig. 3).

Although the species status of Swiss pondweed is controversial (Kaplan, 2008; Wiegleb, 2018), as a perennial species in Lake Constance it clearly differs from *Stuckenia pectinata*, which usually dies off in summer and overwinters as turions and seeds. Swiss pondweed forms much longer shoots than *S. pectinata*, up to 5 m long, only flowers in autumn and rarely bears fruit (Lang, 1967). Therefore, Peintinger (2019) recommends a separate classification regardless of its taxonomic status. According to Baumann (1911), the species he classified as a variation or subspecies of *P. vaginatus* at the beginning of this century mainly occured in the Seerhein, the short river connecting the Upper and Lower Lake (Fig. 3), and also below Eschenz to Schaffhausen in the

Rhine. According to Jaag (1946), in addition to Swiss pondweed (*P. helveticus*), curly-leaf pondweed (*P. crispus*), opposite-leaved pondweed (*Groenlandia densa*) and Canadian waterweed (*Elodea canadensis*) overwinter in the flow area of the Seerhein. In 1967, Swiss pondweed was found in the Seerhein and the connecting flow channels of the Seerhein in the Ermatingen Basin (Jaag, 1968; Lang, 1973). Its presence at the outflow of the Lower Lake near Stein am Rhein was also confirmed, whereas Swiss pondweed was no longer found in the Bay of Constance. In 1978 the location in the Seerhein and connecting channels in the Ermatingen Basin were confirmed, while no examples were found in the Bay of Constance or near Stein am Rhein (Lang, 1981). During a dive in January 1989, Schmieder and Kiechle only found Swiss pondweed sporadically in the Ermatingen Basin, but exclusively in channels of the Seerhein, at the upper edge of the channels. The channels themselves were completely free of vegetation. These observations were documented again in 1993 (Schmieder, 1998); also in 1993 the channels of the Seerhein in the Ermatingen Basin were still practically completely free of vegetation. In shallow areas in the Rhine channels in the Bay of Constance, I. Kramer found evergreen shoots of the species in 1994 (personal comm., cited in Schmieder, 1998). Mapping the Swiss Lower Lake in 2009 (Dienst and Strang, 2010) revealed that Swiss pondweed had multiplied compared to the investigation in 1993.

The question therefore arises as to whether the increase in *P. helveticus* is the main cause of the change in water level differences. To clarify this, the spread of wintering stocks of *P. helveticus* was mapped in March 2017 in the Seerhein from the Bay of Constance to Ermatingen. Subsequently in the summer of 2017, the Swiss Federal Office for the Environment (BAFU) commissioned a reassessment of the entire water vegetation in the area of the Seerhein with the adjoining areas of the Bay of Constance and the eastern part of the Ermatingen Basin, as well as the outflow of the Rheinsee (Eschenz) (Dienst et al., 2017). In addition, dives were carried out to document the shoot lengths and densities of *P. helveticus*. A hydrodynamic model was created using the module Delft3D-FLOW of the Delft3D software suite (Deltares, 2014), which takes into account the flow resistance due to macrophytes in three dimensions, to mathematically estimate the influence of macrophytes on runoff conditions and water levels in Lake Constance.

2. Location of the study area

The study areas lie in the outflow of Lake Constance Upper Lake, the Seerhein and the outflow of the Lower Lake near Stein am Rhein (Fig. 3). Mapping in March 2017 recorded the wintering stocks of *P. helveticus* in the Seerhein to Ermatingen. The Seerhein and Ermatingen Basin are traversed by channels several meters deep. Large areas in the Bay of Constance are relatively flat and determine the discharge threshold of the Upper Lake. On the western edge of the bay there is a deeper, pothole-like area. Due to the narrowing and elevation of the lake floor,
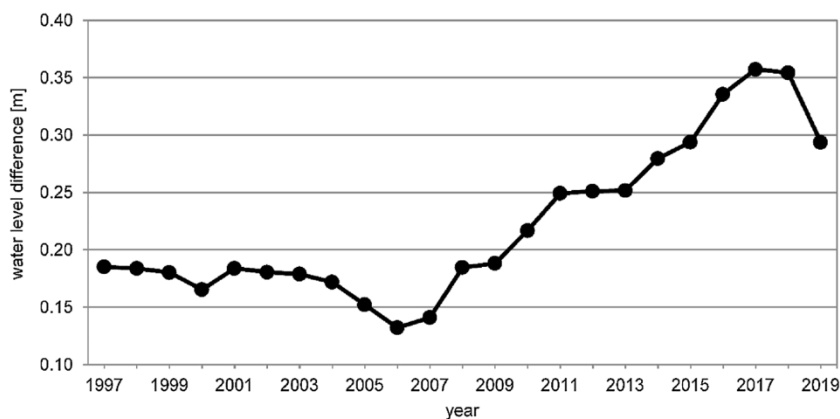

Fig. 1. Changes in water level differences between the Upper Lake (Constance level) and Lower Lake (Radolfzell level) over 20 years. Data source: LUBW (State Institute for the Environment Baden-Württemberg). The zero water level was newly determined for the Radolfzell level in 2017, resulting in a value 6 cm lower than before. Accordingly, the difference values shown here would have to be increased by a total of 6 cm. However, since the new zero point is in doubt and is currently being checked, values in relation to the previous zero point are shown here. The zero point of Constance amounts to 391.895 m a.s.l. and that of Radolfzell to 391.894 m a.s.l. within the height system DHHN92 (HS 160).
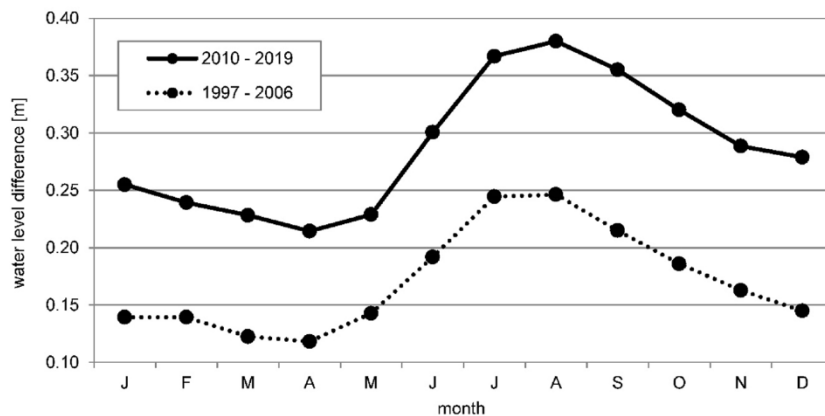
Fig. 2. Differences in the height of water levels between the Upper and Lower Lake in individual months over two time periods. Data source: LUBW (State Institute for the Environment Baden-Württemberg). Note the explanation for the Radolfzell zero water level point is given in Fig. 1.
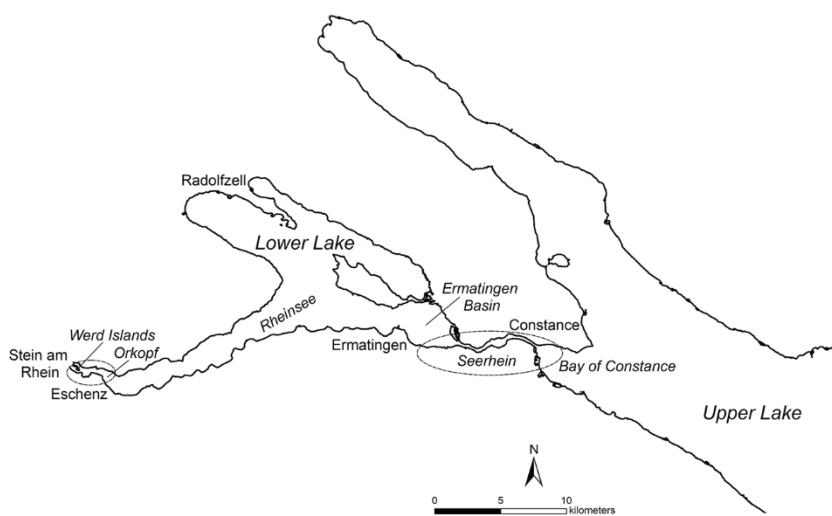

Fig. 3. Location of the two study areas in the outflow areas of Lake Constance Upper Lake in the Bay of Constance / Seerhein and Lower Lake near Stein am Rhein.
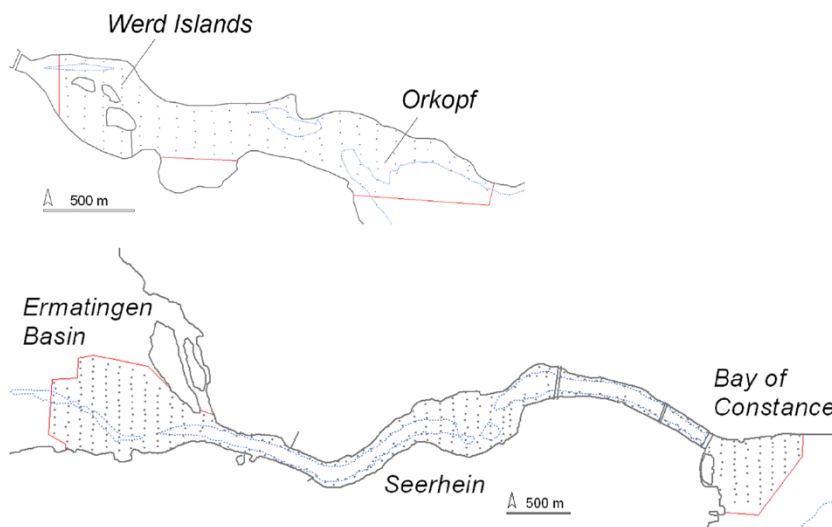

Fig. 4. Location of the sampling points of the survey in summer 2017 (n = 532). Blue dotted line indicates a depth of 8 m (Source: Teiber, 2001), i.e. limits of growth depth of submersed vegetation (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

the current leading to the Seerhein increases continuously. For the summer mapping in 2017, the outlet of the Lower Lake between Eschenz and Stein am Rhein was also mapped (Figs. 3, 4). Also a flow channel and constriction here leads to a strong current.

3. Methods

3.1. Assessment of the study area

The mapping was carried out according to the methodology of Schmieder (1998) in order to ensure that all the data can be compared. In 1993, the submerged macrophytes of the entire Lake Constance were mapped in transects usually 50 m apart with sampling intervals of 50 m along the length of the transects. When the current mapping was carried out, transects were created at a distance of 100 m; within transects, samples were again taken at intervals of 50 m (Fig. 4). Where banks were very narrow, sampling did not strictly adhere to transects, but followed a zigzag pattern. The mapping was carried out in the period from March 17–18, 2017 and July 17 until August 14, 2017. At the sample points, three to four random samples of the vegetation around the boat were taken using plant hooks, and the plants pulled out were identified on site.

Plant amounts was documented as follows (Kohler, 1978; Melzer, 1988):

1 = very rare (only individual plants)
2 = rare
3 = widespread (moderately available)
4 = frequent
5 = abundant (dominant)

The depth was measured by markings on the plant hook rope. The use of a handheld depth sounder proved not practical due in part to the dense vegetation. Sample point locations were recorded with a GPS device (GARMIN etrex 30, UTM, WGS 84). The measured depth values were given according to the current water levels in relation to the mid-water at the Radolfzell water level =313 cm (reference: 1997–2010) or at the Constance water level =331 cm (reference: 1980–2010, data source: LUBW State Institute for the Environment Baden-Württemberg).

3.2. Evaluation of the field data

The GPS sample point data were entered into ArcGIS (version 10.4, ESRI Redlands CA). The mapping data were digitized in MS Excel and linked to the geometric data of the sample points using the GPS position data. This was used to create distribution maps for the individual species. For frequency comparison with 1993, the percentage of the total collected plant mass was compared for each recorded species. A distinction was made between the four sub-areas of the Bay of Constance, the Seerhein, Ermatingen Basin and Rheinsee/outflow (see Fig. 3). For comparison with the current survey, the data from 1993 (Schmieder, 1998) were available in GIS. Changes in the trophic state during the investigation period were interpreted using the macrophyte trophic state indicator values of the different species (MPI) according to Melzer (1988). The indicator values span from 1 (oligotraphentic) to 5 (eutraphentic).

3.3. Diving investigations

To investigate the population density and growth height of the *P. helveticus* stocks and their effect on the water current, several dives were carried out by research divers in the Bay of Constance, the Seerhein and at Orkopf near Eschenz, in parallel to the mapping work between July 17 and August 14, 2017. A number samples of *P. helveticus* shoots were taken, packed in plastic bags, and shoot length was measured in the laboratory. Shoot densities were estimated in different stocks during the dive by counting the shoots in several decimeter squares and extrapolating them to one square meter.

3.4. Hydrodynamic modeling

A hydrodynamic model was created for the outflow area of Lake Constance Upper Lake into the Lower Lake in order to simulate the flow conditions and water level gradient between the two parts of the lake. Using a model component that depicts the flow resistance of macrophytes, simplified scenarios with different macrophyte cover were calculated to assess the resulting water level difference between the two lake basins and the changes in the vertical profiles of the flow velocity. The hydrodynamic model was created using the module Delft3D-FLOW of the Delft3D software suite (Deltares, 2014). The topography of the model grid is based on a high-resolution digital ground model (IGKB, 2016). The horizontal grid width was 5 m; vertically the grid was divided into 10 topography-based layers (sigma layer model) with a refined grid division towards the bottom. The hydrological boundary conditions were chosen so that the water level in the Upper Lake and the outflow quantity into the Lower Lake were specified based on the observed values for the long-term mean water relationship.

In the initial phase of calculating such a model, the water level of the Lower Lake changes until the inflow from the Upper Lake – depending on the changing gradient between the Upper and Lower Lake – corresponds to the specified outflow from the Lower Lake. The resulting water level difference between the two parts of the lake is evaluated for several scenarios with different macrophyte growth and compared with the observed actual water level changes. In addition, the effect of the macrophytes on the horizontal flow velocities was assessed by comparing the model results between the different scenarios. To represent the Upper and Lower Lake as sufficiently large reservoirs, and thus avoid feedback and numerical artifacts from the water flowing in or out, a simple rectangular basin area with low spatial resolution was used for the inflow and outflow areas in the model, to save computing time. The macrophytes are taken into account by a three-dimensional vegetation model. The flow resistance of the aquatic plants acts in the water column, and thus depicts the vertical flow profile better than simpler model approaches, which only work with increased surface roughness. The aim of the basic studies carried out here was not to investigate the hydraulic effect specifically for *P. helveticus*, but to obtain an estimate of how an example of macrophyte cover in selected areas could affect the water levels. We therefore assumed a simple vegetation height of 40 cm and 100 plant stems per m^2 with a diameter of 1 mm each.

For the hydrodynamic model studies, three scenarios (S1 to S3) with different macrophyte cover were examined (Table 1). S1 has no macrophytes; S2 defines vegetation on area A2 in the middle section of the model, and in S3 there are 3 macrophyte areas (A1 to A3; see Fig. 12). Selection of the vegetation areas was based on initial observations of resettlement of dense stocks of Swiss pondweed, as well as considering in which areas macrophytes are particularly effective for causing congestion. Due to the shallower depths in A1 to A3 compared to the deeper flow channels in between, these are threshold areas where increased flow resistance can be particularly effective in raising the water levels.

Table 1

Configuration and results from the model studies on the influence of macrophytes on the water level difference ΔW between the Upper Lake ($W_{Upper\ Lake}$) and Lower Lake ($W_{Lower\ Lake}$). Q is the outflow rate from the Lower Lake, or the inflow from the Upper to the Lower Lake in the equilibrium state of the model run.

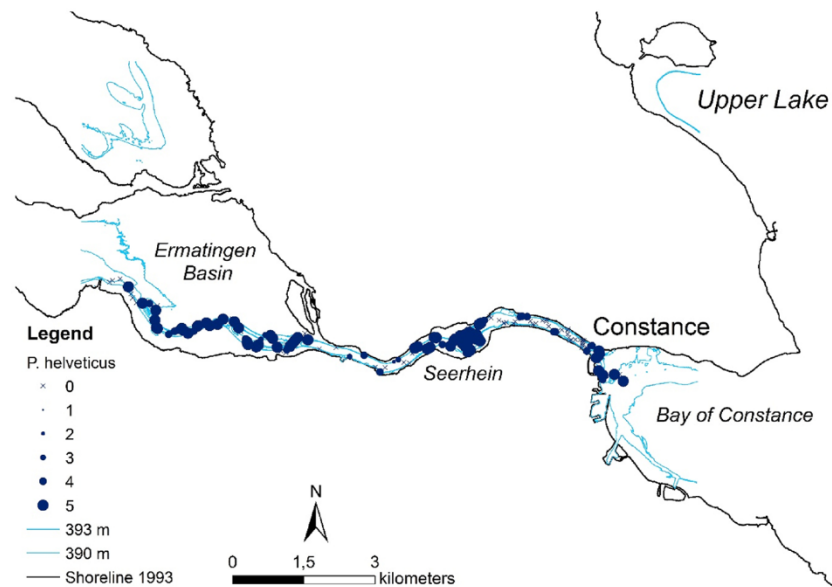| Model studies		Q [m^3/s]	$W_{Upper\ Lake}$ [m a.s.l.]	$W_{Lower\ Lake}$ [m a.s.l.]	$|\Delta W|$ [cm]
S1	no macrophytes	362	395.21	395.04	17
S2	1 macrophyte area	362	395.21	395.02	19
S3	3 macrophytes areas	362	395.21	394.91	30

Fig. 5. Results of late winter mapping of the evergreen stands of *P. helveticus* from the Bay of Constance on the eastern edge of the map through the Seerhein to Ermatingen on March 15 and 16, 2017. The plant quantity data refer to the Kohler (1978) scale.

Table 2
Overview of the submerged macrophyte species recorded in the study area in 2017 and 1993 and their macrophyte trophic state indicator value (MPI) according to Melzer (1988).

Scientific name [1]	English name	1993 number of samples out of 790	percentage 1993	2017 number of samples out of 532	percentage 2017	MPI [2]
Flowering plants						
Alisma gramineum	Ribbon-leaved water-plantain	9	1.14%	0	0	3.5
Ceratophyllum demersum	Rigid hornwort	1	0.13%	2	0.40%	5
Elodea canadensis	Canadian waterweed	1	0.13%	21	3.90%	5
Elodea nuttallii	Nuttall's waterweed	0	0.00%	23	4.30%	5
Groenlandia densa (= *P. densus*)	Opposite-leaved pondweed	4	0.51 %	16	3.00%	3.5
Myriophyllum spicatum	Spiked water-milfoil	0	0	7	1.30%	3
Najas intermedia	Intermediate naiad	0	0	5	0.90%	3
Potamogeton crispus	Curled pondweed	2	0.25%	0	0	4.5
Potamogeton friesii	Flat-stalked pondweed	3	0.38%	0	0	5
Potamogeton helveticus (= *Stuckenia helvetica*)	Swiss pondweed	4	0.51 %	165	31.00%	3
Potamogeton lucens	Shining pondweed	13	1.65%	6	1.10%	3.5
Stuckenia pectinata (= *Potamogeton pectinatus*)	Fennel pondweed	447	56.58%	184	34.60%	4
Potamogeton perfoliatus	Perfoliate pondweed	97	12.28%	135	25.40%	3
Potamogeton pusillus (= *P. panormitanus*)	Lesser pondweed	252	31.90%	22	4.10%	3.5
Potamogeton trichoides	Hairlike pondweed	0	0	4	2.60%	4
Potamogeton × salicifolius (= *P. × decipiens*)	Willow-leaved pondweed	0	0	14	0.80%	3.5
Ranunculus trichophyllus	Thread-leaf crowfoot	25	3.16%	17	3.20%	4.5
Zannichellia palustris	Horned pondweed	188	23.80%	126	23.70%	5
Nuphar lutea	Yellow water-lily	2	0.25%	0	0	4
Nymphaea alba	White water-lily	1	0.13%	0	0	4
Stoneworts						
Chara aspera	Rough stonewort	16	2.03%	44	8.30%	1.5
Chara contraria	Opposite stonewort	566	71.65%	227	42.70%	2.5
Chara dissoluta (= *Ch. denudata*)	Naked stonewort	3	0.38%	1	0.20%	2.5
Chara globularis (= *Ch. fragilis*)	Fragile stonewort	261	33.04%	256	48.10%	2.5
Chara tomentosa	Horn-leaved stonewort	0	0.00%	10	1.90%	2
Nitella opaca	Dark shiny algae	0	0.00%	2	0.40%	2.5
Nitellopsis obtusa	Starry stonewort	3	0.38%	19	3.60%	2.5
Filamentous algae						
Cladophora sp.	Green algae	121	15.32%	6	1.10%	5
Enteromorpha sp.	Turf green seaweed	6	0.76%	0	0	5
Hydrodictyon sp.	Water network algae	2	0.25%	0	0	5
Spirogyra sp.	Screw algae	136	17.22%	66	12.40%	5
Vaucheria sp.	Tube algae (large)	1	0.13%	13	2.40%	5

[1] Characeae according to AG CHARACEEN DEUTSCHLANDS (2016), flowering plants according to BUWAL and INFOFLORA (2016).
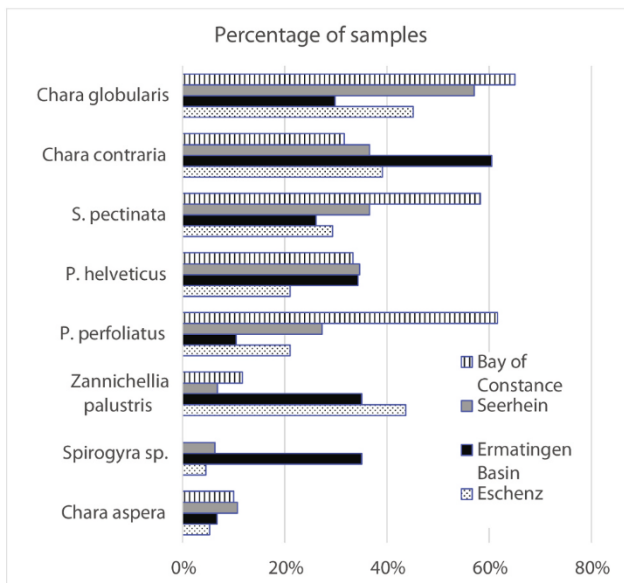[2] MPI = macrophyte indicator value according to Melzer (1988).

Fig. 6. Percentage of the eight most common macrophyte species from 2017 within the total number of samples in the four sub-areas.
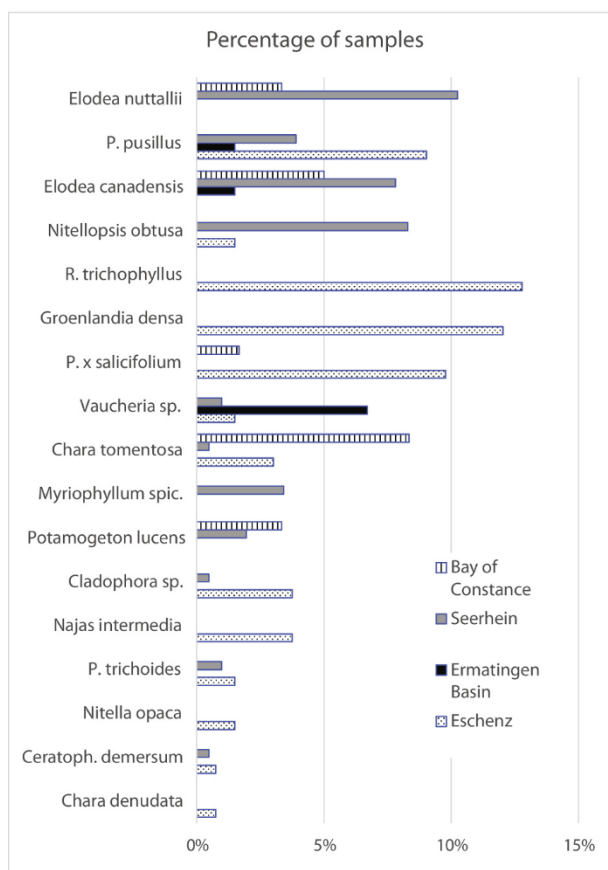

Fig. 7. Percentages of 17 less frequent macrophyte species recorded in 2017 within the total samples in four sub-areas.

4. Results

4.1. Abundance of P. helveticus in March 2017

The assessment of Swiss pondweed in mid-March 2017 showed that the species is abundantly represented in the Seerhein and Ermatingen Basin to the west to Ermatingen (Fig. 5). The occurrence of *P. helveticus* is mostly limited to the strongly flowing channels of the Seerhein and the Ermatingen Basin. Particularly in the Bay of Constance, at the bottleneck and on the eastern edge of the Ermatingen Basin, dense stocks are found down to the bottom of the channels. However, in Ermatingen (on the western edge of the map in Fig. 5), the occurrence of *P. helveticus* appears to be lower. Overall, at the sampled points *P. helveticus* only grew in clearly flowing areas, and most vigorously in the strongest flow areas at the entrances to the corresponding channels, from approx. 1.5 m to 6 m depth, and also covered the channel bottom up to this depth. Deeper channel areas were not covered. In more shallow, weakly flowing areas outside the channels, the species was mostly overgrown by epiphytic algae and less vigorous.

4.2. Submerged macrophytes in the study area in 2017 compared to 1993

An overview of the species found in summer 2017 compared to 1993 shows some special features (Table 2). *P. helveticus* shows a high abundance, accounting for 31 % of all 532 samples, which is only surpassed by *S. pectinata* (34.6 %) as well as *Chara contraria* (42.7 %) and *C. globularis* (48.1 %). *P. helveticus* is spatially restricted to the strongly flowing areas of the Seerhein and Rhine channel, as the mapping of evergreen species in March 2017 shows (Fig. 5). In comparison to 1993, *P. helveticus* increased from 0.51 % of samples in 1993 to 31 % in 2017. In contrast, the following species have declined compared to 1993: *S. pectinata, Potamogeton pusillus, Chara contraria, Cladophora* sp. Some species that still existed in 1993 could not be found in 2017: *Alisma gramineum, Potamogeton crispus, P. friesii, Nuphar lutea, Nymphaea alba, Enteromorpha* sp. and *Hydrodictyon* sp. However, we did find the last two species in 2017 in other areas of the Lower Lake. *Alisma gramineum* actually appears to be in decline, as does the neophyte *Enteromorpha* sp. The species newly discovered in the study area compared to 1993 were *Myriophyllum spicatum, Najas intermedia, P. trichoides, P. × salicifolius, Chara tomentosa* and *Nitella opaca*.

When comparing the four sub-areas (Figs. 6 and 7), the following special features stand out: *P. helveticus* is relatively evenly represented, while *P. perfoliatus* is only comparatively well represented in the Bay of Constance. The eutraphentic species *Zannichellia palustris* (MPI = 5, see Table 2), *Spirogyra* sp. (and also *Chara contraria*) only occur frequently in the Ermatingen Basin.

Ranunculus trichophyllus, Groenlandia densa and *P. × salicifolius* are typical species in the river-like outflow near Eschenz (Fig. 7). The comparatively frequent occurrence of *Ch. tomentosa* in the Bay of Constance is striking. In fact, it was rediscovered there during the mapping after several decades of absence. The species has become common again for more than 10 years in parts of the Lower Lake.

The percentage of individual species within the total samples was assessed according to the frequency in 2017 (Fig. 8). According to this, *Chara globularis* and *Chara contraria* represent the most common species. In contrast to *P. helveticus, S. pectinata* has decreased significantly. Other eutraphentic species (compare MPI values in Table 2), such as *P. pusillus* and *Cladophora* sp. have also decreased compared to 1993. *Chara contraria* can also be regarded as nutrient tolerant compared to other Characeae.

4.3. Shoot lengths and shoot densities of P. helveticus and effects of plants on the current

Swiss pondweed grows in stocks with up to several thousand sprouts per square meter at the bottom of channels (Fig. 9) at a depth of up to 6
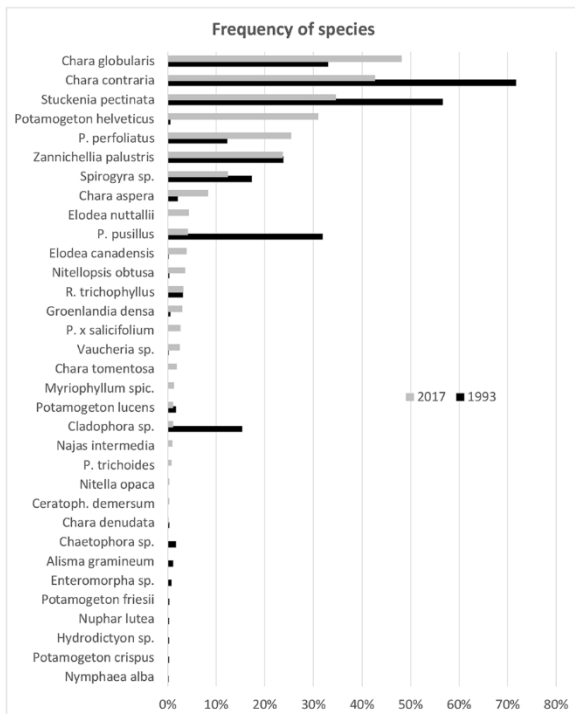
Fig. 8. Percentage of plant species occurring in all samples (1993: 790; 2017: 532) sorted by relative frequency in 2017. The last eight species only occurred in 1993.

m of water, as well as at the slope edge and also in small stands in isolated adjacent areas.

The plants were sometimes more than 5 m long in the flow channel and float up to about 1 m below the water surface. The flow-calming effect of stocks of Swiss pondweed in the channels of the Seerhein was clearly evident at the base of the plants. While a very strong water current was evident on the water surface, and divers could hardly hold their position without a safety line (Fig. 10), hardly any current was felt in stands near the bottom of the channels, and a safety rope was not necessary to examine the shoot densities. Due to the floating movements of the plants, turbulent currents were clearly visible on the water surface. In addition, there are also large stocks of stoneworts (mostly *C. globularis*) that are up to one meter high. Clasping-leaf pondweed (*P. perfoliatus*) also forms dense stocks – especially in the Bay of Constance and in the central part of the Seerhein (compare Fig. 11). However, they do not grow on the bottom of the channels, only at their edges and adjacent shallow water flow areas. The plants are pressed down by the current and do not float in the entire water column like *P. helveticus* (compare Fig. 11).

4.4. Modeling the effects of macrophytes on the hydrological regime of the outflow of Upper Lake Constance

In the model scenario S1, where no macrophytes were present, a water level difference of $|\Delta W| = 17$ cm would occur between the two sub-basins of Lake Constance (Table 1). This corresponds to approximately the mean water level difference before the observed spread of Swiss pondweed (Fig. 12). In scenario S2 with a macrophyte cover in area A2, there is only a slight increase in $|\Delta W|$ by 2 cm (not shown in Fig. 12). In contrast, the three vegetation areas A1 to A3 in scenario S3 result in an increase of 13 cm compared to S1. This means that $|\Delta W| = 30$ cm in S3, which is within the range of recent conditions, which increased to a maximum of $|\Delta W| = 36$ cm by 2017 (Fig. 1).

Evaluation of ΔW along pathline L (Fig. 12) shows that the areas A1 to A3 are regions in the Seerhein with increased flow resistance and thus
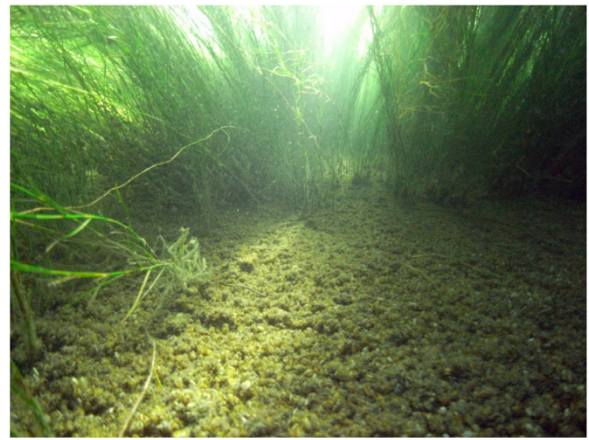

Fig. 9. Sprout densities of *P. helveticus* in the flow channel at the bottleneck of the Bay of Constance, 2017 Oct. 12th.

Fig. 10. Diver holding on to a safety line above stocks of *P. helveticus* at the bottleneck of the Bay of Constance (Area A1 in Fig. 12), illustrating the strong current in the top layer, Oct. 12, 2017.

Fig. 11. Vegetation stocks on the edge of channels in the center of the Seerhein (Area A2 in Fig. 12). In the foreground stocks of *P. perfoliatus* pressed down by the current. In the background, floating stocks of *P. helveticus* in the flow channel, Oct. 11, 2017.
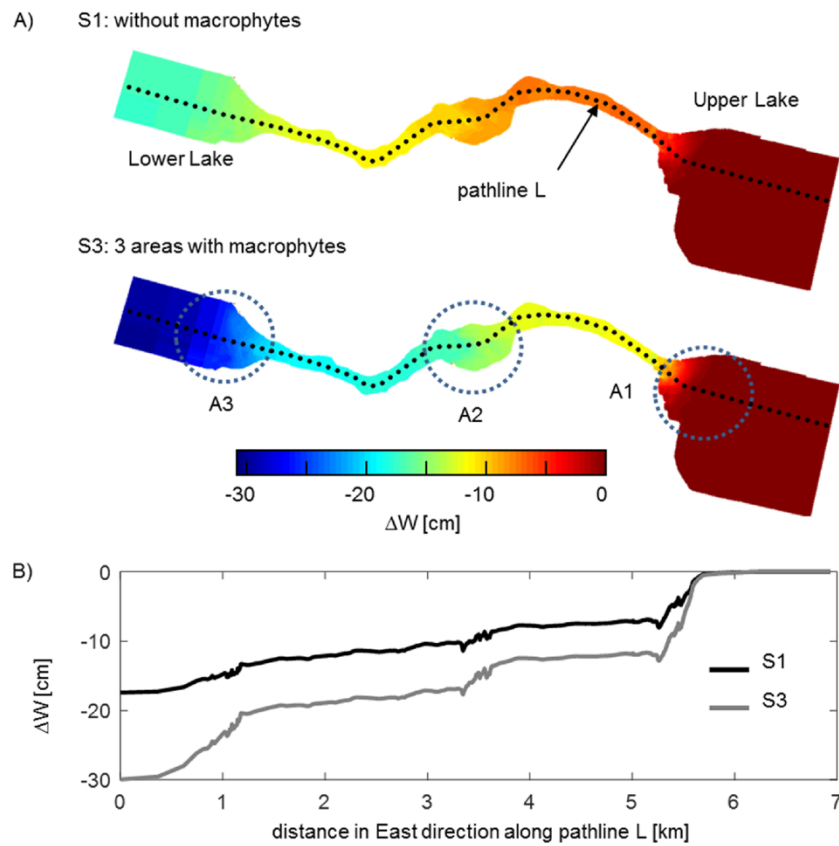
A)   S1: without macrophytes

Fig. 12. Representation of the calculated water levels between the Upper Lake (right) and the Lower Lake (left) for the model scenarios S1 and S3 given as water level difference ΔW related to the Upper Lake water level $W_{\text{Upper Lake}}$. The circles in A roughly indicate the position of the macrophyte areas A1 to A3. B plots the water levels along the east coordinate of pathline L delineated in diagram A.
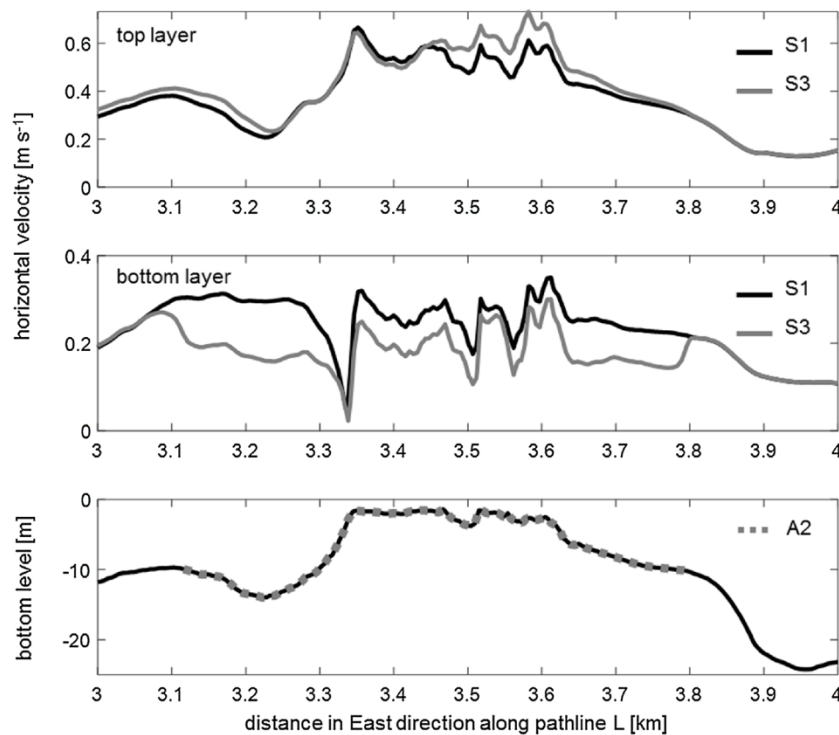

Fig. 13. Comparison of horizontal velocities in the top layer (upper panel) and the bottom layer (middle panel) in area A2 along pathline L (see Fig. 12) for the two scenarios S1 (no macrophytes) and S3 (areas with macrophytes). The lower panel shows the bottom level given as depth below the water level of Upper Lake Constance, i.e. depth below 395.21 m a.s.l. The grey dotted line depicts the area of the macrophyte patch A2 along pathline L.

larger water level gradients compared to the deeper channels in between these areas. Comparison of scenario S1 and S3 shows that the macrophytes increase the water level gradients in these areas and thus the total water level difference between the Upper Lake and the Lower Lake. These larger water level gradients lead to higher flow velocities in the upper layers of the Seerhein flow. In contrast, flow velocities in the in the deeper water layers are attenuated by the flow resistance of the macrophytes. Using area A2 as an example we observe an increase in the flow velocities in the upper layer of up to 14 cm s^{-1} along L or a relative increase of up to 26 % (Fig. 13). In the bottom layer we find a decrease of up to 14 cm s^{-1} or a maximum relative drop of 69 %. However, also in the upper layer there are areas with a slight reduction in flow velocities (e.g. at about L = 3.35–3.45 km), indicating two- or three-dimensional changes in the streamline pattern of the velocity field. The low velocities in the bottom layer at the distance point of about 3.33 km are related to the comparably sharp drop in the flow bed (Fig. 13).

5. Discussion

The main question is what has caused the changes in water level differences between different parts of Lake Constance since 2007. While water level differences showed a significant negative trend in the 20th century (LUBW, 2011), the differences have increased again since 2007.

Our studies provide clear evidence that the sharp increase in Swiss pondweed has been the major cause of increased water level differences at least since 2009. The dense and very high floating stocks significantly increase the flow resistance in water channels, which results in raising the water levels. Indeed, the strong influence of the dense high-growing stocks of Swiss pondweed on the current in channels of the Seerhein was clearly felt during the dives. The congestion effect caused by aquatic plants is a phenomenon that has long been known in many rivers (Gils, 1962; Kahnt et al., 1989; Sand-Jensen et al., 1989; Sand-Jensen and Pedersen, 1999; Trepel et al., 2003; Bal et al., 2011). In relation to the study area, important questions are: what is causing the large spread of *P. helveticus,* and how could the growth previously restricted to the edges of the channels spread out to the bottom of the channels, and also to areas outside the channels in the Bay of Constance and in Ermatingen Basin.

According to Lang (1967), *P. helveticus*, in contrast to *S. pectinata*, blooms late, from the end of August to November, and fruiting rarely occurs. A targeted search for flowering or fruiting shoots of *P. helveticus* in the Seerhein area on Oct. 19, 2020 was not successful. Therefore, vegetative spread is predominant. Crumbling of the channel edges formed from lake chalk certainly occur repeatedly, which can transport rooted plant material weighed down with sediment components to the bottom of the channels. However, light conditions during times of high trophy may not be sufficient to establish stable colonization at the bottom of a channel. The extreme year 2003 with very low summer water levels could have played a decisive role in this. The shallower water in the Seerhein may have favored the breakdown of channel edges by ship traffic. In areas with less flow outside the channels also plant fragments may have spread and established.

The rediscovery of oligotraphentic stoneworts that have been lost for decades (Dienst and Schmieder, 2004; Dienst and Strang, 2009; Dienst et al., 2012; Murphy et al., 2018) proves that Lake Constance trophic levels have been significantly reduced as a result of nutrient load reduction and improved waste water management in the catchment area (Güde et al., 1998). The significantly improved light conditions have enabled submerged vegetation to spread to deeper areas of the shallow water zone since the mid-1990s (Schmieder, 1998; Dienst and Strang, 2009, 2010; Dienst et al., 2017). For example, initial stocks that reached the bottom of the channels could have vegetatively spread over the following years and led to the increases in water level differences that can be measured from 2007 onwards. Alternatively, climate change over the past decades, with rising water temperatures (Straile et al., 2003; Güde and Straile, 2016, 183 ff.), could also have led to changes in the

phenology of Swiss pondweed, and therefore increased the importance of distribution via seeds. Indeed, a spread upstream, e.g. as found in the Bay of Constance, can in any case only be explained via vectors such as waterfowl distributing shoot parts or seeds (Coughlan et al., 2017; Reynold and Cumming, 2016). In summer months, water level differences are also significantly higher than in winter months due to seasonal abundance of other submerged aquatic plant species. However, the congestion effect of these plants is mainly limited to the shallower growth areas outside the channels. Stoneworts are also increasingly remaining green over winter, but these calm the flow and cause sedimentation on the lake floor outside the channels only (Mainberger and Schmieder, 2020).

Since the distinction between *P. helveticus* and *S. pectinata* is not always easy due to the range of morphological variations, the species status is controversial (Kaplan, 2008; Wiegleb, 2018), but sampling in the winter half-year simplifies mapping of the evergreen stocks of *P. helveticus*. However, according to Kaplan (2008) and Wiegleb (2018), *S. pectinata* also partially forms evergreen stands. In Lake Constance, both taxa also grow mixed together in the shallow water zones adjacent to the Seerhein channels. While here *S. pectinata* blooms and fruits in June, populations of *P. helveticus* bloom in autumn, and according to Lang (1967) rarely produce fruits. The above-ground shoots of *S. pectinata* also often die already at the end of July, while *P. helveticus* remains green over winter under the same site conditions in situ. Also, shoots collected during the campaign in March 2017 have stayed evergreen in a tub until today. These phenomena speak against site-related variants of one species. However, in contrast to the Seerhein, where *P. helveticus* remains green over winter, the plant growth areas recorded as *P. helveticus* in the summer of 2017 seem to largely die off in winter at Orkopf near Öhningen. Thus the research diving groups of the State Monument Office and Office for Archeology of the Canton of Thurgau were easily able to investigate the uncovered sites as part of a cooperation project that lasted until 2018 (Mainberger and Schnyder, 2013; Benguerel et al., 2020). Local fishermen also confirm that Orkopf is hardly overgrown in winter, so one can conclude that the plants recorded there were *S. pectinata*. Ultimately, only genetic studies of the two taxa can clarify the question. Due to the different ecology and effects on the water level in parts of Lake Constance documented in the present study, we, as well as Peintinger (2019), therefore advocate a separate recording regardless of the taxonomic status. Comparing the abundance of the aquatic plant species in the present survey with the 1993 survey in the study area showed a significant decrease in eutraphentic species such as *S. pectinata* in favor of oligotraphentic species such as stoneworts, which are currently growing to a depth of 14 m. This confirms that light conditions have improved and the trend of oligotrophication has continued in the study areas. This trend was also found in studies of Lake Constance as a whole (Murphy et al., 2018). Increased braking of the currents usually results in stronger turbulent currents dissipating flow energy. Indeed, during the field studies intense turbulent currents could be observed at the water surface in areas with dense macrophyte stocks. Since the observed stocks of *P. helveticus* are mostly considerably higher and more dense than the macrophytes specified in the simulations, the braking effect of *P. helveticus* on the flow velocities should be stronger than that of the macrophytes in the model. However, the floating behavior of the long shoots of *P. helveticus* reduces hydraulic resistance, whereas only inflexible macrophyte stands could be represented in the model. Using the present model and mapping data, the hydraulic effects of macrophytes can now be investigated in more detail. More specific information about macrophyte stocks can now be specified in the model to allow more realistic simulations that are closer to actual conditions.

Colonization of the channels by Swiss pondweed leads to significant habitat changes in the outflow areas. Reducing the flow close to the ground impairs the living conditions for sessile filter feeders such as the zebra mussel (*Dreissena polymorpha*). Forming large mussel beds in the channels annually over the past decades, these represent an important

food source for winter-resting water birds (Jacoby and Leuzinger, 1972; Werner et al., 2005). Furthermore, by changing the flow velocities, Swiss pondweed alters the habitat conditions that it depends on itself. It may extend its colonization area by increasing flow velocities in areas with previously unsuitably low velocities in the vicinity of the flow channels. Alternatively, decreasing velocities, for example in the flow shadow of Swiss pondweed, could help other macrophytes settle in areas previously not suitable for them.

The flow reduction near the ground, as observed during mapping and confirmed by our model simulations, leads to a corresponding reduction in the bottom shear stresses responsible for erosion processes. For example, sediment accumulation has been found in the Bay of Constance where previously erosion had been destroying archaeological sites (Benguerel et al., 2020; Mainberger and Schmieder, 2020).

Rising water levels could also have consequences for plant communities on the Lake Constance shoreline, such as reed beds and the Deschampsia rhenana community, an endemic lakeshore plant community, which is phytosociologically described as Deschampsietum rhenanae. The Deschampsia rhenana community grows on gravelly bank sections with a gradient of about 1:10 to 1:30 in the height range from approximately the mid-water line (Constance 331 cm) to approximately 50–60 cm above this (Strang et al., 2012). Various monitoring surveys carried out over the past three decades on the Baden-Württemberg and Swiss shores showed that individual plants react differently to extreme water levels (Strang et al., 2012). Overall, after the low water phase in 1989/1990, beach turf has spread extensively towards the lake. The types of Lake Constance forget-me-nots (*Myosotis rehsteineri*), shoreweed (*Littorella uniflora*) and shore buttercups (*Ranunculus reptans*) were able to expand and thus significantly increase their numbers. Only the Lake Constance tussock grass (*Deschampsia rhenana*), which is endemic to Lake Constance, could not follow this trend. It was not able to shift towards the lake so quickly and was displaced on the landwards side by competing plants. For beach turf, a significant increase in Upper Lake water levels can be critical, since many shallow water areas are restricted on the landward side due to built-up structures. This means the populations cannot move inland, and the habitat of beach turf may be permanently reduced. Already a reduction in seasonal water level fluctuations, as can be observed as a consequence of climate changes (Straile et al., 2003), is reducing the habitat of beach turf.

The lakefront of the reed bed is about 50 cm (max. up to 100 cm) lower than that of the *Deschampsia rhenana* community. Aquatic reed stocks react negatively to strong floods in spring, as was the case in 1965 and 1999, since juvenile reeds can only survive for a very short time submerged underwater (Schmieder et al., 2004; Dienst et al., 2004). Over the last 15 years, the reed bed has been able to expand again towards the lake (Ostendorp and Dienst, 2012). The reeds (and also other reed species) can adapt to increasing water level differences over the short term, but early floods are critical. Milder winters caused by global warming lead to increased winter water levels and could lead to earlier floods in spring, which could impair the aquatic reeds.

The hydrological observations do not currently indicate any further increase in water damming due to macrophytes. In a long-term comparison, the current water level differences are about as large as at the beginning of the 20th century (LUBW, 2011). In accordance with reports from Baumann (1915), (1925), (1928), this suggests that the development is due to aquatic plant populations recovering in outflow areas; these probably declined over the course of the 20th century due to eutrophication of Lake Constance. The development documented here is a good example of the resilience of submerged macrophytes.

6. Summary

One reason why water level differences between the Upper and Lower Lake have notably increased in recent years may be due to the observed increasing numbers of aquatic plants, which slow down water movement and thus lead to a congestion of water. Therefore, it seemed expedient to carry out aquatic plant mapping in the relevant areas and to compare this with the mapping results from 1993. In addition, a computational estimate of how macrophytes can influence water runoff behavior and water levels was carried out using a three-dimensional hydrodynamic model. In March 2017 and from July 17 to August 14, 2017, submerged macrophytes in the Seerhein near Constance and Rheinsee near Eschenz were mapped under commission from the Swiss Federal Office for the Environment BAFU. The survey in summer 2017 included sampling carried out by divers.

The studies show that Swiss pondweed (*P. helveticus*) has increased at least more than five-fold since 2009, and is responsible for the change in water runoff behavior and year-round increase in water levels. It grows with up to several thousand shoots per square meter at the bottom of flow channels at up to 6 m water depth, as well as at the edge of the channels and also in small stands in adjacent shallower areas. The plants were usually several meters long, sometimes up to 5 m long. At the same time there are large stoneworts stocks that are over one meter high. Clasping-leaved pondweed (*P. perfoliatus*) also forms a dense population – especially in the Bay of Constance. Trophic changes and climate change are discussed as the cause of increased Swiss pondweed growth in the outflow areas of Lake Constance. However, the exact mechanisms of the spread are not known and require further investigation.

The hydrodynamic simulation results correlate closely with the observed water level changes, and not only help to identify bottleneck areas of the flow, but also support our understanding of the related hydrological processes. The macrophytes lead to reduced flow velocities near the bottom, while water movement is accelerated in the upper water layers due to the increased water level gradients induced by the macrophytes. Based on the presented mapping data, future simulations can be improved to closer fit actual conditions.

The flow-reducing effects of the dense stands of Swiss pondweed not only lead to considerable direct changes in the habitat, but also indirectly to changes in the habitat of the partly endemic shore vegetation due to increased water levels. The current situation is comparable to that at the beginning of the 20th century and thus demonstrates the resilience of submerged macrophytes.

CRediT authorship contribution statement

Klaus Schmieder: Conceptualization, Investigation, Formal analysis, Visualization, Writing - original draft, Funding acquisition. **Bernd Wahl:** Conceptualization, Methodology, Writing - review & editing, Visualization, Formal analysis. **Michael Dienst:** Investigation, Formal analysis, Writing - review & editing. **Irene Strang:** Investigation, Writing - review & editing. **Gunnar Franke:** Investigation, Funding acquisition. **Martin Mainberger:** Investigation, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

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