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Benthivorous fishes interaction with submerged vegetation – A simple enclosure experiment

Abstract

This study tested the setup of an enclosure experiment to exclude or at least diminish direct impacts of medium- to large size benthivorous fishes on submerged macrophytes in three EU habitat type 3140 lakes in NE-Germany. In lakes Großer Glietzen and Peetsch no effect on stimulation of regrowth of macrophytes could be observed, the enclosures remained free of macrophyte vegetation like the reference plots. This is likely caused by water level fluctuations resulting in lake bottom conditions unsuitable for macrophyte development. Only in Lake Stechlin significant differences of macrophyte development between inside and outside the enclosure have been observed in 2014 and 2015. The ratio of covered vs. uncovered sediment was significantly influenced by presence or absence of benthivorous fishes. Also the ratio of charophytes vs. angiosperms and other groups was significantly influenced. In 2014 and 2015 Charophytes dominated the macrophyte vegetation inside the enclosure, while at the reference plot in 2014 angiosperms dominated and in 2015 significantly increased. The experiment results support the hypothesis, that benthivorous fishes are key species and strongly influencing macrophyte communities. Additionally species-specific direct impacts of certain benthivorous fishes on macrophytes are documented from direct observations.

Keywords: submerged macrophytes, charophytes, mesotrophic lakes, enclosure experiment, non-piscivorous fishes.

1 Introduction

Submerged macrophytes play an important role in the community ecology of freshwater habitats, and the presence of vegetation alters the functioning of lakes. Typically, in oligo- and mesotrophic lakes especially, stoneworts (*Charophyta*) dominate submerged macrophyte communities. Generally, the presence of submerged macrophytes is affected by light regime within the water body. Macrophyte vegetation tends to be abundant in clear-water lakes” where especially Charophyte communities occur in specific strata. In contrast, submerged vegetation in lakes with turbid water is usually poorly represented or absent. Water turbidity is almost always linked directly to eutrophication resulting from nutrient influx from the

catchment area. Previous studies have focused on interactions between submerged macrophytes and other autotrophic organisms such as periphyton and phytoplankton, as well as competition between charophytes and angiosperms within a submerged macrophyte community (BLINDOW 1991).

The model of two alternative states was developed for shallow polymictic eutrophic lakes. However today it is also applied to deeper dimictic mesotrophic lakes to explain how turbidity regulates macrophyte appearance (SCHEFFER 2004). Increasing nutrient levels stimulate phytoplankton growth, which in turn leads to higher turbidity, increased light attenuation and a reduction of the maximum depth at which submerged vegetation can grow. This may serve to explain much of the dramatic decline faced by submerged macrophyte communities in general as well as that experienced by the especially numerous charophyte species throughout Central Europe. Eutrophication causes the unfavorable conservation status of habitat type 3140 according to the Habitats Directive of the European Union across its range. However, in some cases charophyte decline can also be observed in lakes, which lack or are subject to minor increases in the level of turbidity and where there is an absence of agriculture in the catchment area (van de Weyer et al. 2009). Here, factors other than vertical light penetration must be responsible for the rapid regime shift and the decline of submerged vegetation. Exclosures are a common tool used in the management of terrestrial ecosystems such as forests to eliminate the effect of ungulates on young trees, for example. We tested the impact of an exclosure setup to exclude the impact of fishes on submerged vegetation during a two-year experiment between May 2014 and October 2015.



Fig. 1: Adult foraging tench (*Tinca tinca*) in Lake Stechlin © Volker Krautkrämer.

2 Goal, study site, material and methods

This study aimed to test how an enclosure experiment could be set to clarify the effects of fishes of medium to large body size on macrophyte communities. There are many hypothetical impacts of non-piscivorous fishes on submerged macrophytes. These include direct consumption, pressure on grazers and zooplankton, selective consumption, increase in sedimentation and physical damage. Understanding the role of non-piscivorous fishes therefore requires a differentiated exploration of the general fish assemblage, as well as on size-dependent ontogenetic niche shifts.

To differentiate these impacts, large sized fishes had to be excluded from study plots. It was not expected, that enclosures would alter the composition of the grazer community and influence the general abundance of periphyton grazers. Thus, the experiment *a priori* set out to test the influence of medium- to large-sized fish. It was anticipated that at least big herbivorous and benthivorous fish had a visible impact on the macrophyte assemblage. Fish can inhibit macrophytes growth of through increased turbidity (MEIJER et al. 1990). Previous studies had shown a decrease in Charophytes in several lakes, especially across the shallow-water assemblages of *Charetum asperae* and *Charetum filiformis*, which are not linked to turbidity (VAN DE WEYER et al. 2009, OLDORFF & VOHLAND 2009, ARENDT et al. 2011). These shallow depths of 10-300 cm are also a preferred foraging stratum for benthivorous fish. Our study design followed the hypothesis that the space occupied by non-vegetated areas inside the enclosure would decrease as result of the absence of digging to forage for for benthic food, a composition shift from more robust to more fragile species of macrophytes, and an insignificant effect on the light regime.

2.1 Study area and site selection

The study was conducted in three lakes (Lake Großer Glietzen, Lake Peetsch and Lake Stechlin) in the nature park “Stechlin Ruppiner Land“, in the District of Oberhavel, Northern Brandenburg (NE-Germany). The area’s (latitude 53°10’ N, longitude 13°02’ E, altitude of lakes = groundwater level around 59,7 m asl) topography is strongly influenced by the Weichselian glaciation, which formed the terminal moraines of the “Frankfurter Staffel“. The area is famous for its high percentage of lakes with low trophic levels. In the northern part of the protected area “Stechlin“, which is at the same time a Special Area of Conservation (SAC) according to the EU Habitats Directive (EU-No. DE 2844-301) and a Special Protection Area (SPA) according to the EU Birds Directive (EU-No. DE 2843-401).

All three lakes are categorized as habitat type 3140 (hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp.), but differ in size and basin morphology. All are endorheic groundwater lakes and have no natural outlets. Only lake Stechlin has an artificial surface outlet, the Polzowkanal. All three lakes have been part of a permanent annual monitoring programme on submerged macrophyte vegetation since 2009 (ARENDT et al. 2011). Presence/absence-data on fish species are available almost only from more than a decade ago (KNAACK & OLDORFF 2006, see table 1). Subsequently, the presence of some species of cyprinid fish has been confirmed (e.g. figure 1).

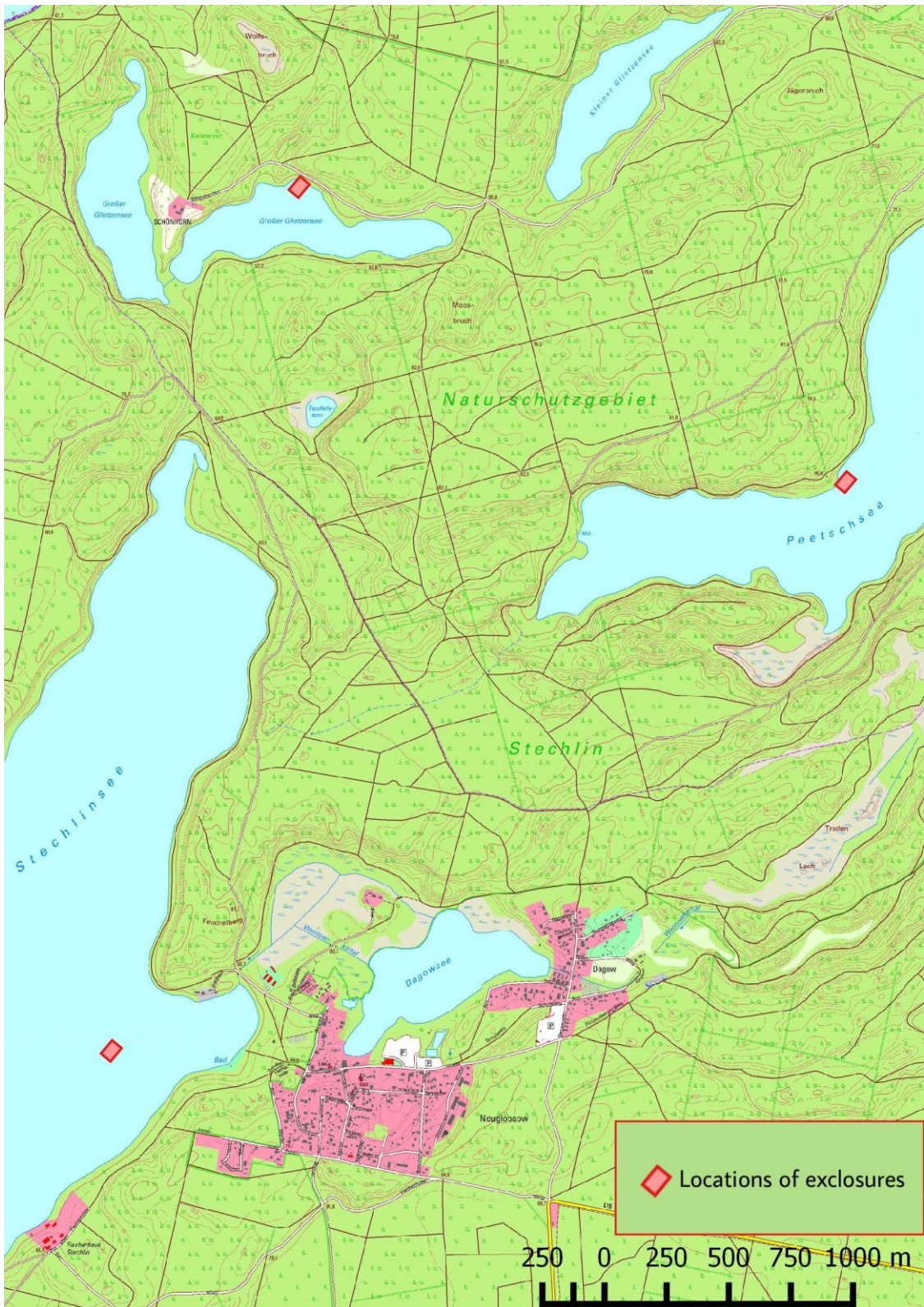


Fig. 2: Map of the study site showing the locations, where exclosures had been installed.

Tab. 1: Presence of Cyprinid fish species in the three lakes (from KNAACK & OLDORFF 2006).

Species	Gr. Glietzen	Peetsch	Stechlin	No. total
Tench (<i>Tinca tinca</i>)	X	X	X	3
Common roach (<i>Rutilus rutilus</i>)	X	X	X	3
Rudd (<i>Scardinius erythrophthalmus</i>)	X	X	X	3
Common bream (<i>Abramis brama</i>)	X	X	X	3
Common Carp (<i>Cyprinus carpio</i>)	X	X	X	3
Silver bream (<i>Blicca bjoerkna</i>)	X	X	X	3
Crucian Carp (<i>Carassius carassius</i>)		X		1
White Amur (<i>Ctenopharyngodon idella</i>)			X	1

2.1.1 Großer Glietzensee (Lake Greater Glietzen)

Lake Großer Glietzen is situated approximately 1.5 km north of Lake Stechlin and consists of two water bodies: an eastern basin covering 20.8 ha and a western basin covering 18 ha, which are separated by a paludifying alder stand. The maximum water depth of the eastern basin is 14 m, the shallower western basin only reaches 11 m. Lake Großer Glietzen is classified as mesotrophic with an average summer Secchi disc transparency of 4 m (KRAUSCH 1964). There are no historic data on submerged macrophytes of this lake, but baseline data have been provided by HOESCH (1996). The water levels of Lake Großer Glietzen vary according to a huge amplitude. The chosen location of the enclosure was in front of the northern central shoreline of the eastern basin. The lake has been part of the macrophyte monitoring programme since 2009. With the exception of single plants of *Myriophyllum spicatum*, vegetation is absent from the shallower, south-exposed parts of the eastern basin (ARENDE et al. 2011). In 2013, recolonization by macrophytes (*Chara tomentosa* +, *Chara globularis* r, *Myriophyllum alterniflorum* 3) had been observed in this part of the lake on a Braun-Blanquet scale. However, by 2014 this part of the lake was again free of vegetation, which is why this area was selected for the enclosure experiment.

2.1.2 Peetschsee (Lake Peetsch)

Lake Peetsch covers 89.1 ha, reaches a maximum depth of 22 m and has an average depth of 10-12 m (an estimated volume of 10-12 million m³). Surface in- and effluents are virtually absent. The lake is classified as mesotrophic and had a submerged vegetation coverage of over 80 percent between 1992-1994. It was home to nine species of charophytes at a maximum depth of 8.5 m (HOESCH 1996) which suffered a dramatic decline in the following years. By 2009, 70 percent of the lake bottom were already free of vegetation, with a dominance of angiosperms, especially *Myriophyllum spicatum* and *M. alterniflorum* (OLDORFF & VOHLAND 2009). Lake Peetsch was added to the annual macrophyte monitoring programme in 2009. Monitoring data (2009-2016) show only minor remnants of submerged vegetation, including only three species of Charophytes. Maximum growth depth was recorded at 6 m with a 75 percent drop in vegetated area.

Water levels of Lake Peetsch are subject to large intra- and inter-annual amplitude changes, with a dramatic drop starting in the mid-1980s. Water levels seem to have stabilized at a very low level since 2003. This water loss coincides with the hydromelioration and drainage of the nearby transition mire area “Traden” (1985-1987), which still contained a cupola shallow lake of 35 ha in 1987. After a short period of stabilization in the beginning of the 1990s, a further period of water level reductions began in 1995. This coincides with the installation of the groundwater supply plant “Dagow” (OLDORFF & PÄZOLT 2010). Since 2000, the annual output of 50.000 to 70.000 m³/a by the water supply plant is equal to 10 percent of the current total calculated groundwater influent (ArcEGMO). In 2010, the lake’s water level sank almost 2 m below the maximum water level of 1982. The lake has lost 22 percent of its water volume (KAISER et al. 2012). The sandy shallow zone at the western shore was selected for the enclosure experiment.

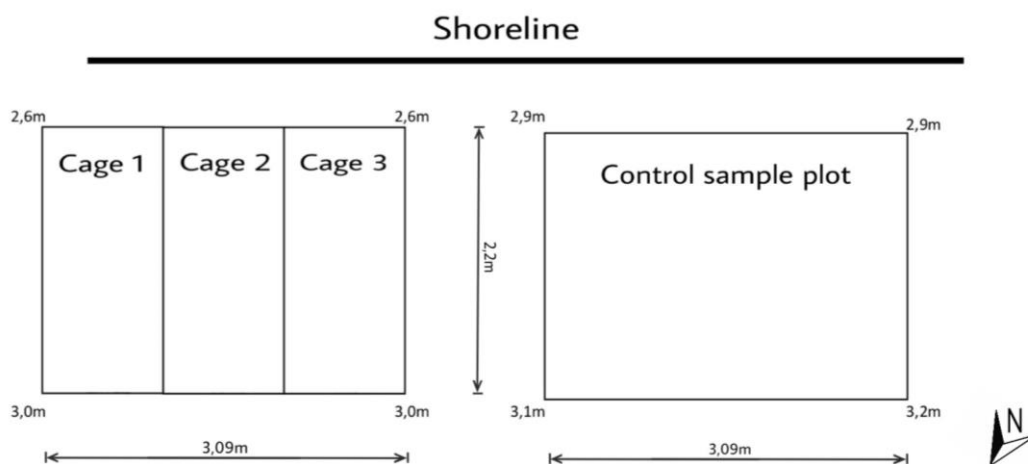


Fig. 3: Schematic representation of the enclosure experiment (Lake Stechlin).

2.1.3 Großer Stechlinsee (Lake Stechlin)

Lake Stechlin covers 425 ha and has a maximum depth of 69 m. This lake is famous for its crystal clear translucent water (steklo Slavic = “glass”). Until quite recently, Lake Stechlin was classified as one of the last oligotrophic clearwater lakes of the Northeast German lowlands. It can still be classified as mesotrophic today. Although its catchment area is almost entirely covered with forest and is strictly protected by law, lake Stechlin’s trophic state and its biological composition have undergone dramatic changes since the 1990s (VAN DE WEYER et al. 2009). The biological structure of lake’s ecosystems is regulated hierarchically. The productivity of several trophic levels is regulated by a variety of interrelated chemical, physical, and biological factors. Two principal non-biological changes have been identified: the depletion of deep-water oxygen concentrations in depths of over 60 m, and a significant and ongoing increase of hypolimnetic phosphorous concentration (KASPRZAK et al. 2010). Multiple factors and long-term effects have been documented and discussed (OLDORFF & PÄZOLT 2010). Prior to the implementation of an annual

monitoring regime in Lake Stechlin, several investigations had documented its submerged macrophyte composition and development.

A baseline study provided by KRAUSCH (1964), reported meadow-like stands of Charophyte associations at a depth of between 0.2 and 20 m. Our monitoring data (2008-2016) show that vast *Nitellopsis obtusa* stands are still present, and stands of *Chara tomentosa* persist locally. However, we also observed vast areas without vegetation where conditions still look suitable. Major losses occurred in the Charetum asperae and Charetum filiformis (shallow-water charophyte communities) as well as in the Nitello-Vaucherietum (deep-water charophyte communities). These communities experienced subsequent losses of over ninety percent (VAN DE WEYER et al. 2009, ARENDT et al. 2011) (macrophyte monitoring 2008-2016). Lake Stechlin has lost nearly 150 ha of submerged macrophyte stands in the last five decades – the equivalent of 80 percent of the former total! As a result of the artificial outlet regulation of the Lake Nehmitz-Stechlin system and the much larger catchment area, water level fluctuations are much less intense in comparison to lakes Großer Glietzen and Peetsch. Interestingly, despite of comprehensive efforts to stabilize water levels since 1999, of the recovery of the water level has been insignificant to date (figure 12).



Fig. 4: Transport of enclosures.



Fig. 5: Installation of enclosure.

2.2 Material and methods

We used commercially available outdoor rabbit cages measuring 220 x 103 x 103 cm, as underwater enclosures. Three of them were joint in order to increase enclosure coverage. We expected edge effects for enclosures of less than 2 m². By combining 3 cages, we were able to reach an effective enclosure size of 6,978 m². The cages are manufactured from stainless steel to provide relative stability. The interval between the struts was 35 mm, which only excludes medium- to large-size fish, but guarantees maximum of light permeability at the same time. A control sampling plot of the same size was marked off with shut-off tape a couple of meters away from each enclosure. Enclosures were installed on 24.05.2014 (Großer Glietzen) 26.05.2014 (Peetsch) and 28.05.2014 (Stechlin). They were checked and maintained regularly, approximately every four weeks. Maintenance included regular cleaning of the cages *in situ*, including the removal of epiphyton to minimize any effects on the light regime. The experiment was scheduled for a period of two years and enclosures have remained in place with regular maintenance and checks for a further season in 2015.



Fig. 6: The impact of large benthivorous fishes on the vegetation outside the enclosures was significant.

3 Results

In two of the lakes (Großer Glietzen and Peetsch), enclosures had no effect on stimulating regrowth of macrophytes and, like the control plots, remained free of macrophyte vegetation. Significant effects on macrophyte development were observed only in Lake Stechlin. In September 2014, the area occupied by *Najas marina* inside the enclosure was significantly lower than in the control plot. At the same time, abundance of charophytes (primarily *Chara intermedia*, *Ch. contraria*, *Ch. globularis*) was significantly higher inside the enclosure. Bare sediment coverage had increased by ten percent under the presence of large fish. In comparison to the enclosure area, Charophyte presence decreased by more than half in the control plot. *Nitellopsis obtusa* disappeared completely outside the enclosure (figure 9).

An interesting first occurrence of gutweed or grass kelp (*Ulva [Enteromorpha] intestinalis*), a salt water and brackish water species, which is only rarely seen in mainland waters (figure 8). It was recorded inside the enclosure in 2014. To our knowledge this finding is a first record of this species in Lake Stechlin. It can be characterized as fragile in terms of the working hypothesis and may have been present in Lake Stechlin and other lakes in the area. It may have remained undiscovered because of an inability to develop stands due to foraging pressure by consumers like fishes. It is also an indicator species for eutrophication.



Fig. 7: The impact of large benthivorous fishes on the vegetation outside the enclosures was significant.



Fig. 8: *Ulva intestinalis* from the enclosure 2014 in Lake Stechlin.

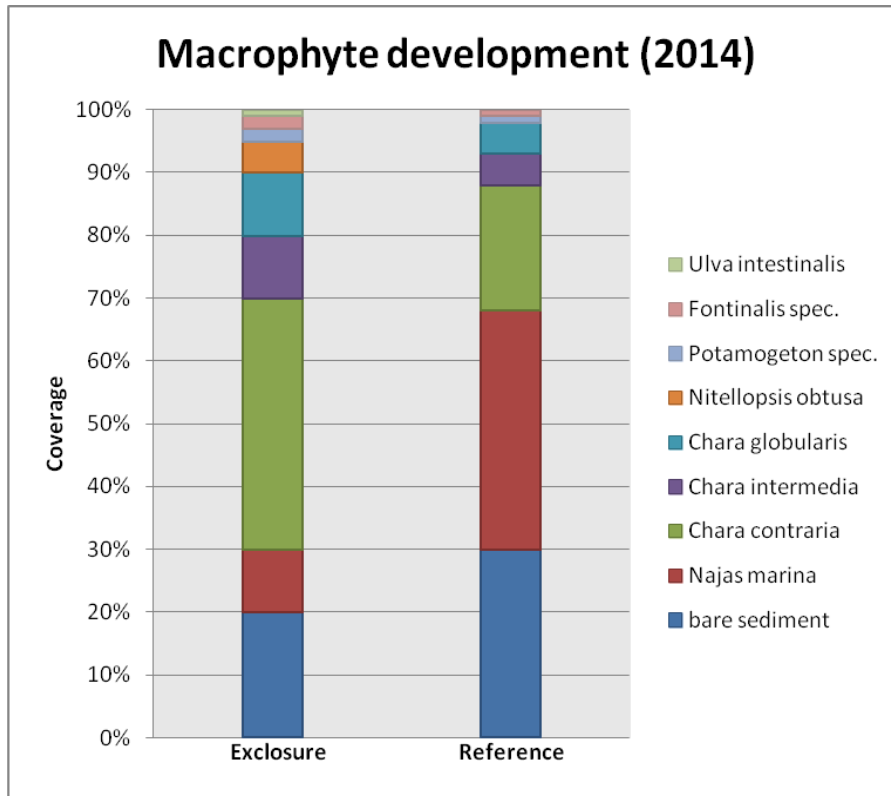


Fig 9: Lake Stechlin enclosure vs. control plot macrophyte coverage 2014.

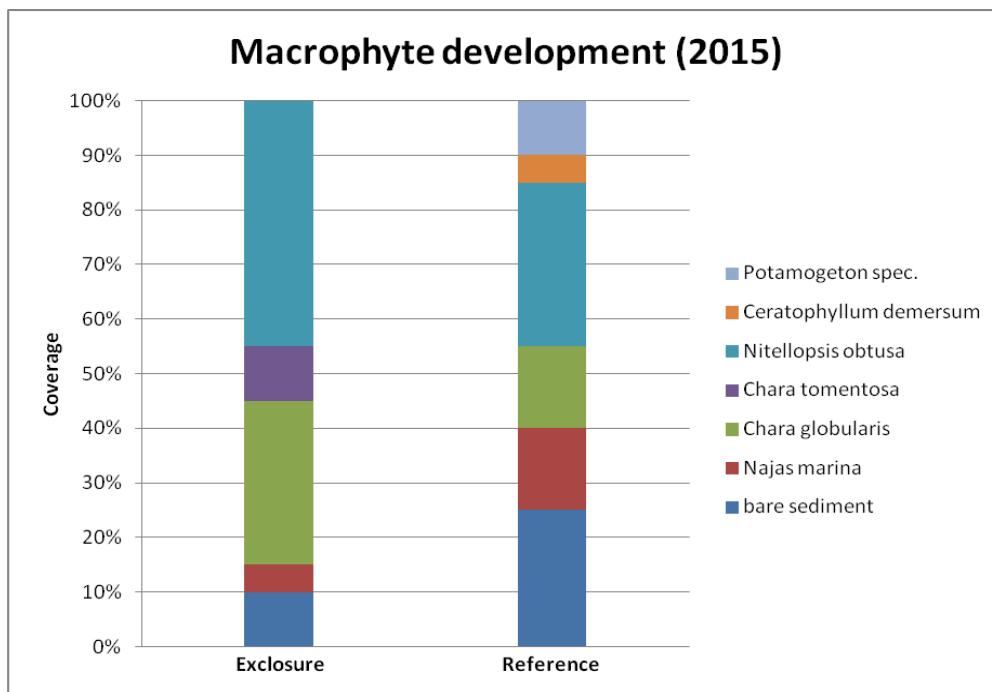


Fig. 10: Macrophyte coverage in the Lake Stechlin enclosure vs. the control plot in 2015.

Species composition in Lake Stechlin was slightly different in 2015, but our results confirmed the hypothesis, that medium- to large size benthivorous fishes have a tremendous effect on macrophyte development (figure 10). Charophytes covered 85 percent of the area, inside the enclosure, compared to just 50 percent in the control plot. Outside the enclosure, bare sediment coverage increased by 150 percent and *Najas marina* presence by 300 percent with the presence of large fishes.

Visually, epiphyton colonization in the control plot was higher than inside the enclosure area, especially with regard to *Najas marina* plants. Unfortunately, the study failed to obtain data on the biomass of these functional and taxonomic groups to verify this colonization.

4 Discussion

No obvious answer as to why enclosures in Lake Peetsch and Lake Großer Glietzen remained free of macrophyte vegetation like the control plots could be identified by this particular experimental setup. The effects of decapod crayfish foraging by the invasive *Oronectes limosus* can be dismissed as a possible explanation as densities are relatively low in both lakes. The most likely explanation in both cases is that the substrate is unsuitable for macrophyte development. This may be a result of sedimentation processes or the physical characteristics of the sediment following significant water level fluctuations (see figure 12). In the case of Lake Peetsch, previous studies had documented the collapse of submerged vegetation between 1992 and 2009 (OLDORFF & VOHLAND 2009).

The water levels of many lakes in Northeastern Germany have shown a dramatic decrease and have suffered intensive fluctuation over the past six decades (see Kaiser et al. 2012). In the case of the lake Stechlin, these fluctuations have initially been influenced by large-scale hydromelioration activities, including the complex drainage of watersheds which are exacerbated by climate-change and land-use patterns in the catchment areas (Oldorff & Pätzolt 2010). A drop in water-level leads to a reduced influx of calcium ions and mobilization of nutrient fluxes.

For Lake Stechlin, our results show a high variability between study years (2014 and 2015). In both years, a decrease of charophytes was observed outside the enclosure, while angiosperms and areas free of macrophyte vegetation increased significantly outside the enclosure.

Whole-lake experiments in the US to determine causality and severity of impacts by carp (*Cyprinus carpio*) on submerged macrophytes have illustrated the species-specific effects of benthivorous fishes (BAJER et al. 2016). Numerous studies have demonstrated that large-size benthivorous fish in particular, have a tremendous effect, which had previously been underestimated. In addition, observations on the species-specific physical effects of certain cyprinid fishes have been reported in lakes of the Stechlin area. They are documented here (figures 13-16) to present the differences between fish species in order to easily identify digging damage associated with different cyprinids.

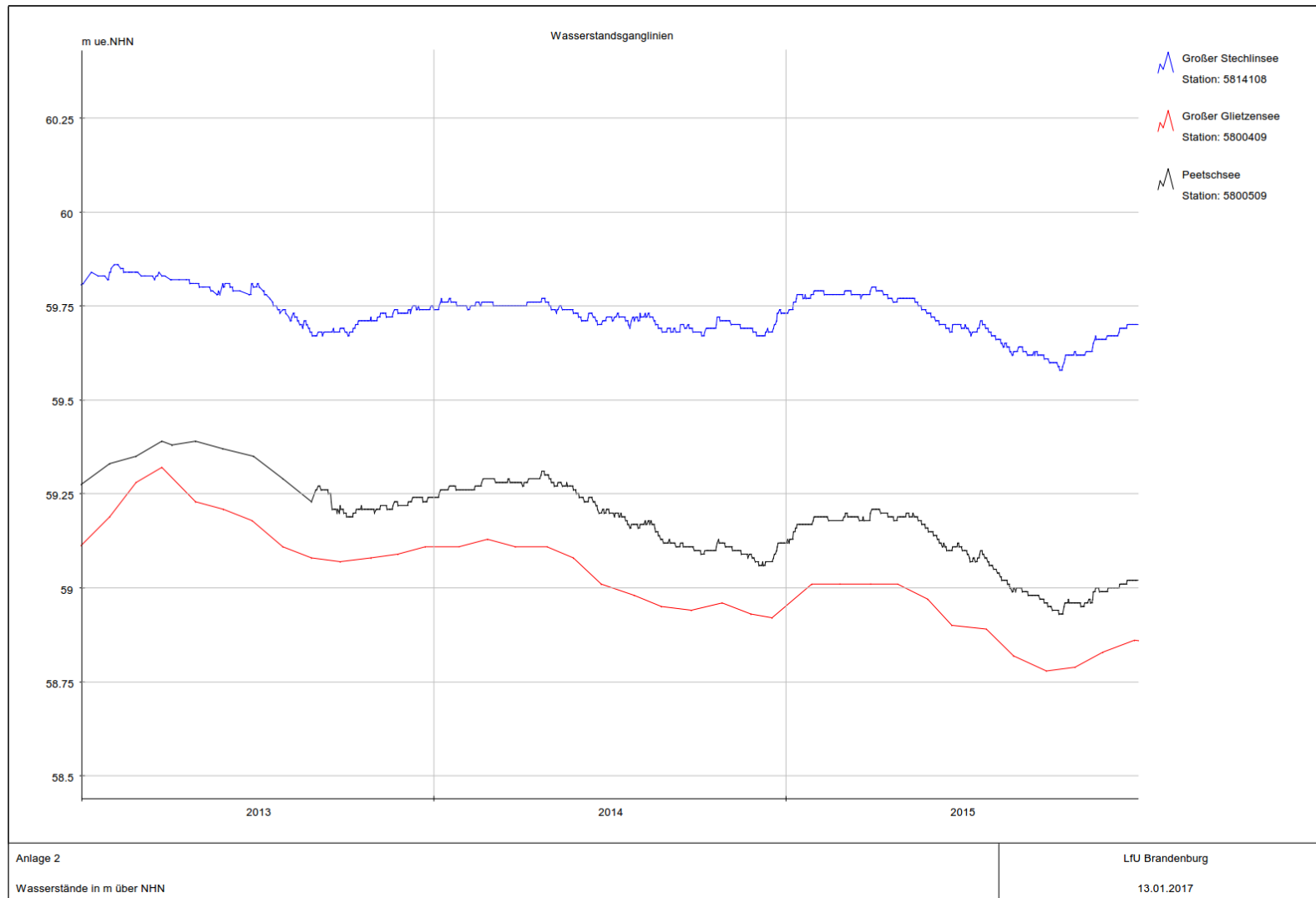


Fig. 11: Water levels of the three lakes in the period 2013-2015.

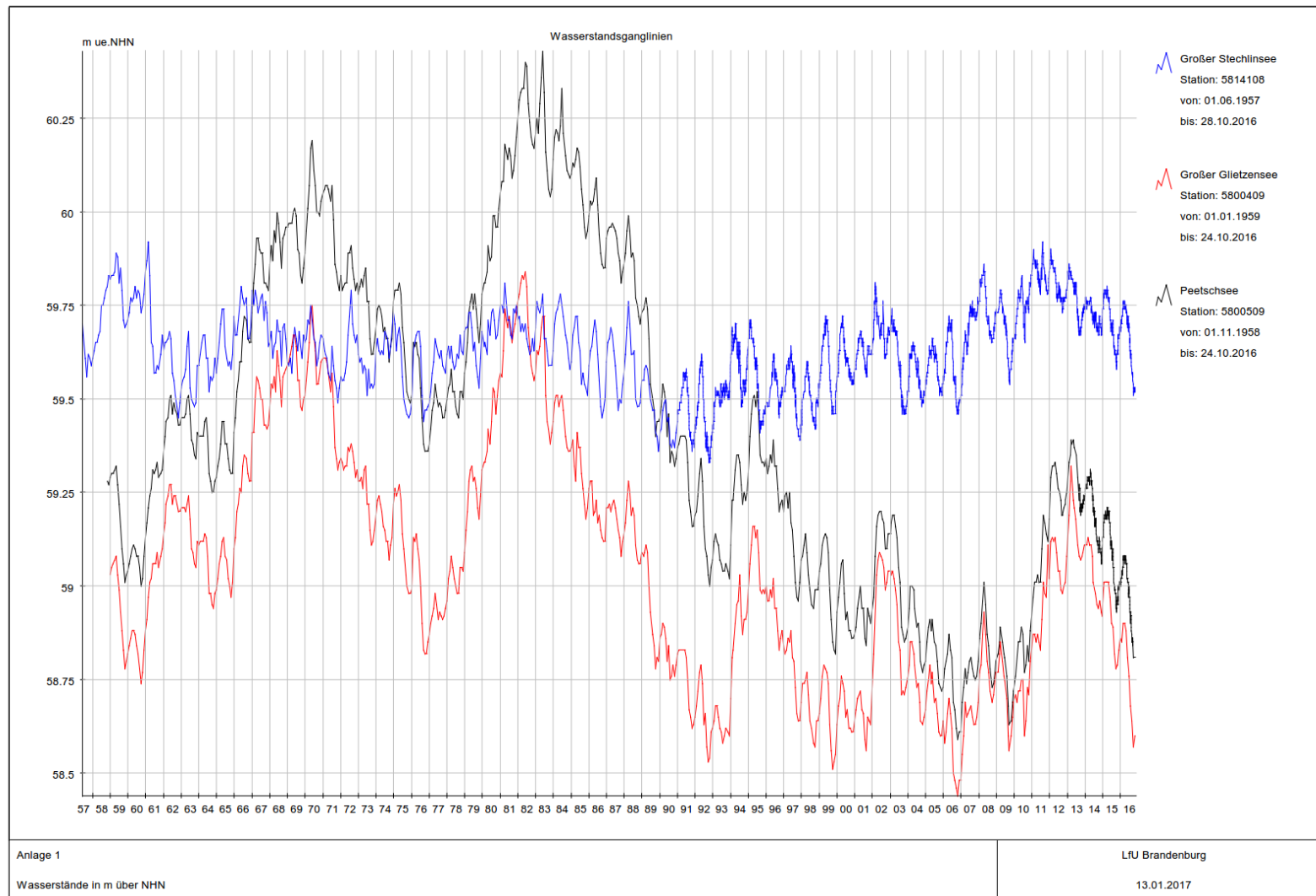


Fig. 12: Long-term water level fluctuations 1957-2016 of the three lakes.

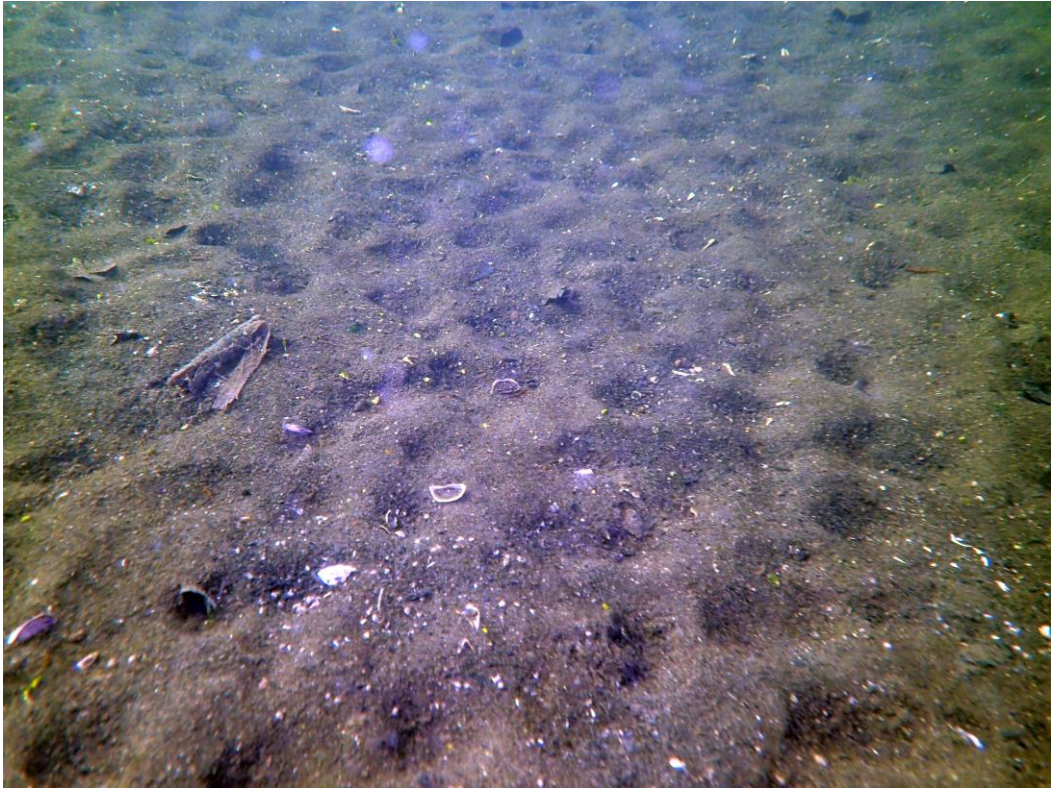


Fig. 13: Digging damage caused by the common bream (*Abramis brama*) in Lake Peetsch.



Fig. 14: Herbivory damage caused by the White Amur (*Ctenopharyngodon idella*) in Lake Stechlin.



Fig. 15: Digging damage caused by the common carp (*Cyprinus carpio*) in Lake Stechlin.



Fig. 16: Characteristic round wholes in the charophyte stands caused by tench (*Tinca tinca*) in Lake Stechlin.

Our results support the view of Meijer et al. (1990) that current approaches to evaluate the impacts of carp and other benthivorous fishes on basis of a biomass per area relation are inaccurate and of little use. Besides their direct physical interaction with macrophytes, benthivorous fish recycle bottom material by releasing sediment nutrients, and through excretion and egestion. In the US, the Eurasian carp is officially classified and managed as an invasive species. However, regrettably, this approach is not adopted in Germany due to the missing element of successful reproduction. Carp do not reproduce successfully in NE-Germany, but are routinely and illegally restocked by humans.

5 Conclusions

Fish interact in multiple ways with submerged lake vegetation and may have a strong impact on macrophytes, including on charophytes. Macrophytes, as well as periphyton, form a food resource for fishes (Prejs 1984). Benthivorous fish in particular, play a pivotal role in even large, deep mesotrophic lakes. Our enclosure study showed that the presence of large benthivorous fish in Lake Stechlin led to a significant decrease of charophytes (e.g., *Nitellopsis obtusa* loss 2014: 100%, 2015: 33%), while angiosperms (especially the hard-leaved *Najas marina* and eutrappent *Ceratophyllum demersum*) and bare sediment increased.

Recommendations:

1. The minimum size of test enclosures should be 5 m². Generally stainless steel constructions performed well in terms of light permeability and stability, but regular maintenance (at least every two weeks), is necessary.
2. Biomass-quantification at the end of the vegetation period should be obligatory. Additionally, epiphyton biomass could be collected for quantification during maintenance.
3. Further investigation of the substrate characteristics of the lake bottom should be set up to determine if it is suitable for re-establishing of lost submerged vegetation.

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