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Review

Causes of macrophyte mass development and management recommendations

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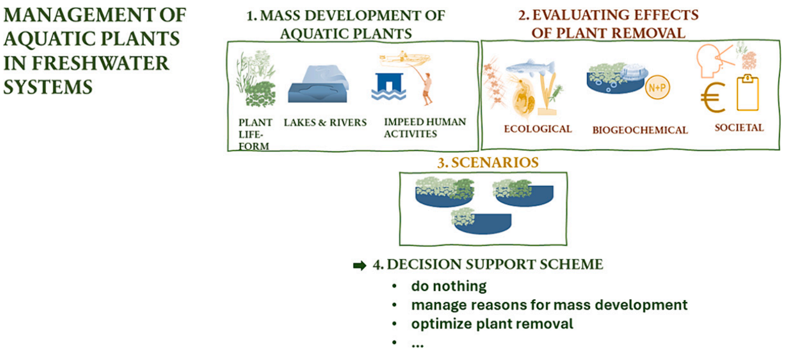
HIGHLIGHTS

- Mass developments of macrophytes are often perceived as nuisance.
- Macrophyte removal is costly and often ineffective.
- We did a standardized set of experiments and questionnaires at 6 sites in 5 countries.
- Macrophyte management often had minimal impact on overall societal value.
- When managing macrophyte mass developments, do not forget the "do nothing" option.

GRAPHICAL ABSTRACT



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ABSTRACT

Aquatic plants (macrophytes) are important for ecosystem structure and function. Macrophyte mass developments are, however, often perceived as a nuisance and are commonly managed by mechanical removal. This is costly and often ineffective due to macrophyte regrowth. There is insufficient understanding about what causes macrophyte mass development, what people who use water bodies consider to be a nuisance, or the potential negative effects of macrophyte removal on the structure and function of ecosystems. To address these

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Nuisance growth
Nutrients
Disturbance

gaps, we performed a standardized set of in situ experiments and questionnaires at six sites (lakes, reservoirs, and rivers) on three continents where macrophyte mass developments occur. We then derived monetary values of ecosystem services for different scenarios of macrophyte management ("do nothing", "current practice", "maximum removal"), and developed a decision support system for the management of water courses experiencing macrophyte mass developments.

We found that (a) macrophyte mass developments often occur in ecosystems which (unintentionally) became perfect habitats for aquatic plants, that (b) reduced ecosystem disturbance can cause macrophyte mass developments even if nutrient concentrations are low, that (c) macrophyte mass developments are indeed perceived negatively, but visitors tend to regard them as less of a nuisance than residents do, that (d) macrophyte removal lowers the water level of streams and adjacent groundwater, but this may have positive or negative overall societal effects, and that (e) the effects of macrophyte removal on water quality, greenhouse gas emissions, and biodiversity vary, and likely depend on ecosystem characteristics and macrophyte life form. Overall, we found that aquatic plant management often does not greatly affect the overall societal value of the ecosystem, and we suggest that the "do nothing" option should not be easily discarded in the management of perceived nuisance mass developments of aquatic plants.

1. Introduction

Freshwater resources are heterogeneously distributed across the planet and are limited in many regions but are central to human life and society (Strayer and Dudgeon, 2010). Multiple threats to freshwater ecosystems negatively affect aquatic biodiversity and availability of water for the well-being of humans, food, and industrial production (see Gleick et al., 2001; Harrison et al., 2016). Indeed, the protection of water resources is central to several of the United Nations Sustainable Development Goals, including "good health and well-being", "clean water", as well as "life below water" and "life on land" (https://sdgs.un.org/goals).

Aquatic plants (macrophytes) play an important role in freshwater ecosystems' functioning, e.g., by promoting biodiversity, ecological interactions, and nutrient cycling (e.g., Jeppesen et al., 1998). Despite their ecological importance, mass development of macrophytes can be an important environmental nuisance (Verhofstad and Bakker, 2019). Non-native (Hussner et al., 2017) and native macrophyte species (e.g., Moe et al., 2013) may both form mass developments, which are publicly perceived as a nuisance. Such mass developments can jeopardize water use, for example hydropower generation, boating, and angling (Verhofstad and Bakker, 2019). Thus, macrophyte removal by mechanical, chemical, or biological methods is a common management measure in reservoirs, lakes, rivers, and streams (see Hofstra et al., 2020 for a perspective).

Existing research devoted to understanding the causes of macrophyte mass developments and the consequences of macrophyte removal generally has focused on specific regions, water bodies, or macrophyte species, or uses meta-analyses (e.g., Thiemer et al., 2021). In addition, management of macrophytes is usually performed without knowledge on nuisance perception of the main users of water bodies nor on economic valuation of different types of use. In a recent study (https://www.niva.no/en/projectweb/madmacs), we performed standardized in situ experiments at six sites where macrophyte mass developments occur, aiming to understand the consequences of macrophyte removal on ecosystem structure, function, and services. The study sites included lakes, reservoirs, and rivers with different trophic levels and uses, and were located in five countries across different climate zones. Macrophytes included submerged, emergent, and free-

Table 1
Description of the study sites (modified from Vermaat et al., 2024). *Negative latitudes are S of the equator; negative longitudes are W of Greenwich. Concentrations of SRP, nitrate, and ammonium (mean + − sd) were quantified in control areas (5–6 replicates per site) before macrophyte removal.

Site (country)	River Otra at Rysstad (Norway)	River Spree from Grosse Tränke to Lake Dämeritz (Germany)	River Guaraguaçu (Brazil)	Lake Kemnade (Germany)	Lake Grand-Lieu (France)	Lake Hartbeespoort Dam (South Africa)
Coordinates (lat/long) *	59.088/7.550	52.430/13.678	−25.6712/−48.5129	51.416/7.260	47.133/1.674	−25.749/27.833
Annual mean discharge (rivers), size (lakes and reservoirs)	69 $m^3 s^{-1}$	14 $m^3 s^{-1}$	3 $m^3 s^{-1}$	125 ha	summer 2700 ha / winter 6750 ha	1850 ha
Important current forms of use	Hydropower, recreation	Recreation, agriculture in the floodplain	Recreation, drinking water	Recreation, hydropower, drinking water, flood regulation	Nature reserve, professional fishermen; recreation and agriculture along its banks	Irrigation, drinking water, recreation
Nutrient status	Oligotrophic	Eutrophic	Eutrophic	Eutrophic	Eutrophic	Hypertrophic
Nuisance species	Submerged, native *Juncus bulbosus* (bulbous rush)	Submerged and emergent, native *Sagittaria sagittifolia* (arrowhead)	Emergent and amphibious, introduced *Urochloa arrecta* (tropical tanner grass)	Submerged, non-native *Elodea nuttallii,* (Nuttall's waterweed)	Emergent and amphibious, non-native *Ludwigia grandiflora* and L. *peploides* (water primrose)	Free-floating, non-native *Pontederia crassipes* (water hyacinth)
Mean plant biomass before removal (g DW m^{-2})	148 ± 35	335 ± 61	692 ± 125	421 ± 180	183 ± 85	972 ± 137
SRP/Soluble reactive phosphorus (μmol L^{-1})	0.0 ± 0.0	3.0 ± 0.4	NA	0.4 ± 0.6	4.2 ± 2.1	21.0 ± 1.1
NO_3^-/Nitrate (μmol L^{-1})	2.5 ± 0.3	22.3 ± 4.8	NA	35.7 ± 14.4	1.8 ± 1.6	105 ± 27
NH_4^+/Ammonium (μmol L^{-1})	1.4 ± 0.3	3.2 ± 0.4	NA	3.0 ± 0.6	14.3 ± 9.2	51.9 ± 23.6

floating plants, which were either native or non-native species to their respective areas (Table 1, Fig. 1). Using a before-after-control-impact (BACI) approach, we measured the effects of the removal of macrophyte mass developments on biodiversity, biogeochemistry, hydrology, and greenhouse gas emissions. Measurements were performed before, one week after, and six weeks after mechanical macrophyte removal. Nuisance perception by users was derived from standardized surveys, while monetary values of ecosystem services were estimated for different scenarios of macrophyte management ("do nothing", "current practice", "maximum removal"). Here, we provide an overview of the project results, extract key insights, and use them to develop a decision support system for the management of water courses experiencing mass developments of aquatic plants.

2. Perception of nuisance growth

We used surveys to obtain data on people's perceptions of macrophyte growth in relation to different user activities (Thiemer et al., 2023). >150 responses were received per study site, except from the site in the River Guaraguaçu (Brazil) from where too few responses were received due to the Covid-19 pandemic. This site was thus omitted from the analysis of nuisance perception.

Negatively perceived macrophyte mass developments ("nuisance growth") is often reported in both scientific and popular media, even though it is largely undefined what nuisance growth is and what drives this negative perception of macrophyte growth (Verhofstad and Bakker, 2019; Thiemer et al., 2023). Perception of nuisance by macrophytes may depend on their cover, biomass, height, life form (submerged, free-floating, or emergent), aesthetics, interference with desired uses, or invasiveness. Other parameters, such as the spatial extent of the macrophyte vegetation (whether mass developments occupy areas that are specifically intended for recreational use), recreational activity (swimming, boating, angling etc.), other ecosystem services provided by the waterway (e.g., food or water source) together with local perception (resident/visitor, environmental orientation) may likewise drive the negative perception of macrophytes. In a thorough literature review, Verhofstad and Bakker (2019) found submerged macrophytes considered to be a nuisance were mainly characterised by a high plant growth rate, being tall, having a high coverage, and forming monospecific mats with high biomass. Our survey results from Norway, Germany, France, and South Africa, spanning different macrophyte life forms, generally support these findings (Box 1; Thiemer et al., 2023). In general, we found that the denser the macrophytes were (in terms of cover and height), the more likely they were perceived as a nuisance. However, we found no single threshold growth level at which macrophytes are perceived as nuisance. Classification of nuisance levels should therefore include site-specific information on the local perception of nuisance (Thiemer et al., 2023).

Current studies suggest that the biggest conflicts of interest are likely to arise when high biomasses of aquatic vegetation occur in water bodies that residents want to use for active recreation (Thiemer et al., 2023; Verhofstad and Bakker, 2019). We found that residents are likely to perceive macrophyte mass developments to be equally or (up to 23 %) more negative than visitors do. Additionally, residents show a higher awareness of the existence of macrophyte mass development in the area (Box 1; Thiemer et al., 2023). The biggest differences between visitors and residents tended to occur at sites where boating was an important recreational activity for residents. Most visitors and residents perceive these macrophytes as a nuisance not only because they interfere with activities such as boating, angling, or swimming, but also because they perceive a negative impact on biodiversity and the beauty of the landscape. Interestingly, an actual negative impact on biodiversity is only partially supported by our study (see section 4.4). Nevertheless, macrophyte mass developments are likely to lead to complaints, first and foremost among the residents that previously used (e.g., River Otra) or want to use (e.g., Lake Kemnade) the water body for active recreation. For water managers it may be difficult to satisfy the local residents' recreational interests when regulating rivers and lakes for energy production or irrigation, since regulation may create a perfect habitat for macrophytes (see section 3.1; Tena et al., 2017).

3. Causes of macrophyte mass development

3.1. Creating a perfect habitat for aquatic macrophytes

Among our case studies and in more general, negatively perceived macrophyte mass developments typically occur in freshwater ecosystems that were anthropogenically modified to suit human needs, and

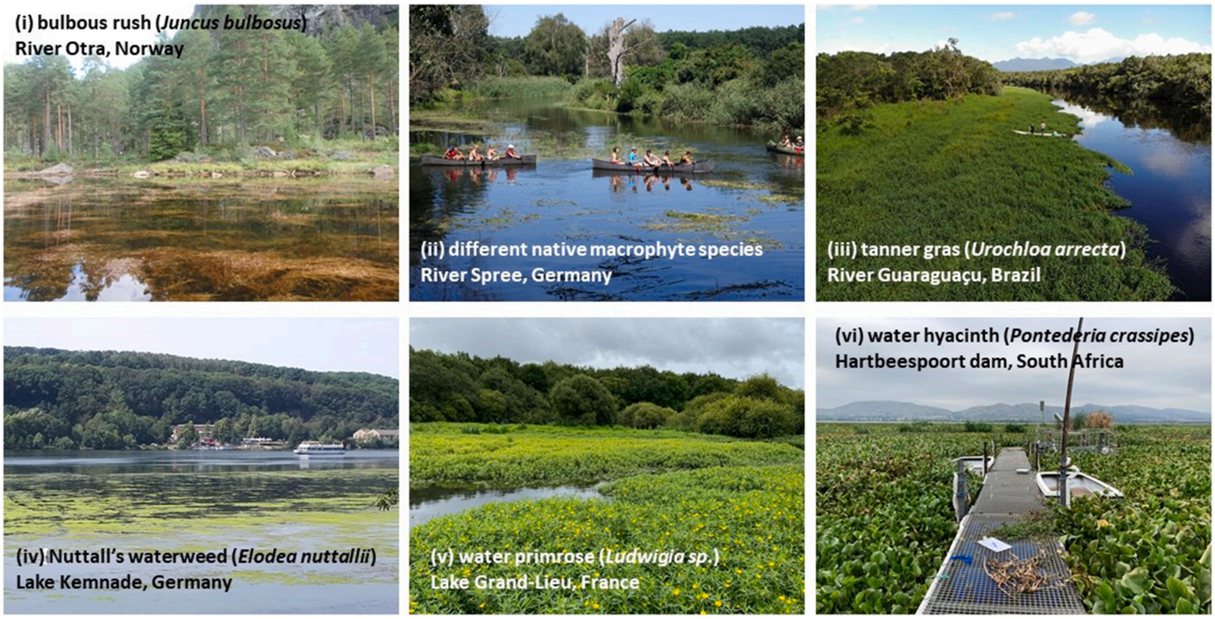

Fig. 1. Macrophyte mass developments occur worldwide and are often perceived as a nuisance. We studied six sites across different climate zones, including lakes, reservoirs, and rivers with different trophic levels and uses. Macrophytes included submerged, emergent, and free-floating plants, which were either native or non-native species. Photos (from (i) to (vi)): S. Schneider, J. Köhler, A. Padial, S. Hilt, B. Misteli, A. Petruzzella.

Box 1

Summary of perception assessments in five case study sites with macrophyte mass developments; based on Thiemer et al. (2023); >150 responses were received per study site; due to the Covid-19 pandemic, too few responses were received from the site in the River Guaraguaçu (Brazil), and this site was thus omitted from the analysis of nuisance perception.

- In the River Otra (Norway), 98 % of residents but only 66 % of visitors perceived the mass development of aquatic plants as nuisance, while in Lake Kemnade (Germany), these numbers were 82 % and 71 % respectively. Both water bodies are intensively used by residents for boating which requires large areas of open water. Visitors perceived the aquatic plants less negatively, possibly because motor boating and sailing were less important activities for visitors than for residents.
- In the River Spree (Germany), 80 % of residents but only 63 % of visitors perceived the mass development of native aquatic plants as nuisance. Both groups expressed concerns about biodiversity. Residents, however, were more concerned about the effect of the mass development on biodiversity than visitors were, and residents perceived high plant biomasses as more negative for angling. The reasons for this are, however, unclear.
- In Hartbeespoort Dam (South Africa), >90 % of both visitors and residents perceived the mass development of the non-native water hyacinth (*Pontederia crassipes* Mart.) as nuisance. People were most concerned about biodiversity, and secondarily about boating and the beauty of the landscape. Hartbeespoort Dam is one of few freshwater bodies that are available for recreation in South Africa, and water hyacinth has been perceived as problematic for decades. The nuisance perception by residents and visitors alike might therefore be related to the fact that people across the country have been aware of the struggle against water hyacinth for decades, combined with the high relevance of this water body for the entire country.
- At Lake Grand-Lieu (France), 75 % of both residents and visitors perceived the mass development of the non-native *Ludwigia* spp. as nuisance. There is little active recreation directly on Lake Grand-Lieu. There are, however, recreational activities in its surroundings, and the lake is mainly valued for its scenic beauty, biodiversity, and birdwatching. The absence of a difference between residents and visitors, and the relatively low nuisance perception among the residents compared to other sites, might be explained by the low importance of active recreation on the lake.

thus – often unintentionally – were turned into perfect habitats for aquatic plants. “Perfect habitat” conditions, however, differ among different macrophyte life forms. The main life form types are free-floating, sediment rooted with emergent and/or floating leaves, and fully submerged (free or sediment rooted). Low light conditions and high turbidity in shallow littoral zones promote dominance of emergent or floating-leaved species, deeper turbid waters favour free-floating species, and submerged plants require sufficiently clear water (Lacoul and Freedman, 2006). In general, standing plant biomass is the sum of all processes related to biomass accrual and biomass loss (Biggs, 1996). “Perfect macrophyte habitats” are therefore generally created by enhancing environmental factors that promote plant growth (nutrients, light, temperature, and carbon availability), or by reducing disturbances that normally cause plant loss (such as floods, droughts, and herbivory) (Riis and Biggs, 2001; Verhofstad et al., 2017). Dams, reservoirs, and diversions (for hydroelectricity or withdrawal) increase water residence time, slowing river flow and/or creating shallow, clear permanent water systems that present the “perfect” conditions for plant species that evolved under such conditions, for example, free-floating macrophytes in the Amazon Basin. Due to particle sedimentation, access to light in the water column is also increased in reservoirs and in ecosystems downstream of dams, which represents an increase in resources for submerged vegetation (Sousa et al., 2009). In general, eutrophication i.e., anthropogenic enrichment of nutrients, typically nitrates and phosphates, also promotes growth of all water plants.

Among the sites we sampled in our study (Table 1, Fig. 1), regulation of the River Otra in Norway has created large shallow, slow-flowing areas that are permanently inundated and little disturbed by floods, droughts, or ice-scraping, promoting perennial growth of the native, submerged macrophyte *Juncus bulbosus* L. despite oligotrophic conditions. Regulation of the River Spree in Germany has created a slow-flowing river that experiences low mechanical disturbance with nutrient concentrations that support nuisance growth of several native submerged macrophytes but not phytoplankton blooms. The River Guaraguaçu is a slow-flowing, tidal, shallow river in Brazil. Nutrient concentrations are high due to poorly treated domestic effluents, particularly during the summer season. Here, *Urochloa arrecta* (Hack.) Morrone & Zuloaga, a non-native perennial grass, can tolerate changing salinity and has a high growth rate, producing a large amount of biomass in a short time, outcompeting native macrophytes. The combination of high nutrient input, relatively slow flows, high turbidity, and rapid development makes these sites ideal for mass development of invasive species. In addition, floating islands of unattached plants created by tidal flows may serve as propagules for new colonisations elsewhere.

In the case of Lake Kemnade (Germany), regulation of the River Ruhr created a nutrient-rich lake with large shallow areas that are little disturbed by floods or droughts allowing mass development of the non-native submerged macrophyte, *Elodea nuttallii* (Planch.) H.St. John. The water level of the shallow Lake Grand-Lieu (France) is managed by a sluice gate, creating large shallow areas that are inundated during winter, while the water level falls towards a minimum during summer. Because the water is turbid, few submerged macrophytes grow (Marion and Brient, 1998). The lake shore, however, is ideal for massive growth of emergent plants, while the nutrient-rich water in the centre of the lake is ideal for floating-leaved and free-floating macrophytes. The construction of the Hartbeespoort Dam on the Crocodile River in South Africa created a reservoir with limited flow and extremely high nutrient concentrations from urban wastewater (Carroll and Curtis, 2021). Due to deep and turbid waters, few submerged macrophyte species grow, but conditions are ideal for massive growth of the free-floating macrophyte species *Pontederia crassipes* and *Salvinia minima* Baker.

From a management perspective, it is important to understand that “perfect habitat” conditions differ among macrophyte species and life forms. They have in common, however, a lack of sufficient disturbance combined with sufficient supply of nutrients, carbon, and light enabling the build-up of plant biomass to nuisance levels. In such ecosystems, both native and non-native macrophytes can form very dense stands and therefore be perceived as nuisance (see Section 2).

3.2. The effect of reduced disturbance in nutrient poor cold freshwater ecosystems

In our experience, the importance of reduced ecosystem disturbance on macrophyte mass development is frequently overlooked. For macrophytes, biomass loss is generally related to hydraulic and grazing factors (Biggs, 1996; Riis and Biggs, 2001; Bakker et al., 2016). Macrophytes generally grow slowly in ecosystems where nutrient availability and water temperatures are low. Nutrient-poor, cold freshwater ecosystems are therefore not generally considered to be at risk for developing macrophyte nuisance growth. Macrophyte mass developments, however, indeed may occur in nutrient poor, cold freshwater ecosystems because many macrophyte species may grow perennially when water temperatures are above zero, light is not limiting, and disturbance level is low. One such example is the Rysstad basin in the River Otra, Norway (Table 1), which experiences mass development of submerged *Juncus bulbosus* (Thiemer et al., 2023). Average plant cover was 64 ± 3 % and average standing biomass 52 ± 16 g C m^{-2} (Demars et al., 2023). The site was nutrient poor (SRP < 3 μg l^{-1}; NO_3^- —N 0.03 mg l^{-1}) and summer-cold (average summer water temperature 9 °C; all measurements June–August 2020). The main growing season of *J. bulbosus* was found to be May to September but photosynthesis was possible year-round (Demars et al., 2023), and most plant biomass generally stays green in winter (pers. obs.). This is possible because regulation of the mountainous River Otra has created a large, slowly flowing, summer-cold and permanently inundated river reach that is little affected by floods or droughts, and which does not freeze in winter. High macrophyte biomass has therefore accumulated over several years (Rørslett and Johansen, 1996).

Net primary production in the Rysstad basin was estimated to be 135 (range: 54–217) g C m^{-2} $year^{-1}$ (Demars et al., 2023). The annual growth of *J. bulbosus* was therefore about 2.6 times its average standing biomass in the Rysstad basin, suggesting large amounts of plant biomass indeed were lost through hydraulic stress, natural mechanical breakage of stems, grazing, or other disturbances, matching personal observations of drifting *J. bulbosus* fragments year-round. These biomass losses, however, obviously did not outweigh plant growth.

Macrophyte mass development in nutrient-rich, summer-warm, regulated rivers is a well-known phenomenon. It is generally related to a combination of high plant growth and reduced disturbance (e.g., Tena et al., 2017). We argue that a risk of macrophyte mass developments should also be considered when regulating nutrient-poor, cold rivers (see Lehner et al., 2011 and Zarfl et al., 2015 for an overview on existing and planned reservoirs and dams worldwide). Many macrophyte species may stay winter-green when water temperatures are above zero, light is not limiting, and disturbance level is low. Such conditions occur e.g., in groundwater-fed streams (Riis and Biggs, 2001), but also downstream of hydropower plant outlets with water intake from large reservoirs (Heggenes et al., 2021). When assessing the risk of macrophyte mass developments in regulated, nutrient poor ecosystems, it is therefore important to take the potential plasticity of macrophyte growth form and life cycle into account and assess if these plants have potential to grow perennially in the newly created freshwater ecosystem.

4. Consequences of macrophyte removal

Even when the causes of macrophyte mass development are known, they are often difficult to tackle by water managers. Nuisance growth of dense macrophyte stands has therefore led to a range of management and control measures (Pieterse and Murphy, 1990; Hussner et al., 2017; Hill and Coetzee, 2017; Thiemer et al., 2021), of which mechanical harvesting is likely most common worldwide. Since macrophytes also provide ecosystem services (Boerema et al., 2014, Janssen et al., 2021, Vermaat et al., 2024), it is important to be aware of potential negative consequences of macrophyte removal.

4.1. Macrophyte removal may reduce water level, but this can be good or bad news

In rivers and streams, dense stands of macrophytes narrow the cross-sectional area of flow and induce turbulence around stems and leaves, slowing river flow. Therefore, dense plant stands elevate the upstream water level at a given discharge. We analysed long-term data on discharge, water level and macrophyte biomass and established water level – discharge relationships to calculate the impounding effect of macrophytes (see Baattrup-Pedersen et al., 2018). In the studied section of the River Spree, Germany (Table 1), rooted macrophytes elevated the mean water level by 60 to 90 cm (averages June–July 2011–2021), and slowed the mean flow velocity by 35 % (Jan Köhler, unpublished results). The impounding effect developed alongside plant growth, starting in April and fading out in October, when plants withered. When river discharge is high, this impounding effect may locally increase flood risk (Gurnell and Midgley, 1994).

When rivers and streams have low to moderate discharge, however, the impounding effect of macrophytes may be beneficial. The increased heterogeneity provides additional habitats and may encourage biodiversity (see Section 4.4). Patchiness and reduced mean flow velocity seasonally increase particle retention (Verschoren et al., 2017). By keeping the stream water level high, the groundwater table in the adjacent floodplain is also raised. In the River Spree, changes in river water level were reflected in the groundwater within a few hours (Lewandowski et al., 2009). Due to the elevated channel and groundwater levels, the water volume stored in the river section roughly doubled (Jan Köhler, unpublished results). Water retention generally helps prevent droughts, and higher groundwater level reduces the mineralization of contiguous fens and the subsequent emission of CO_2, dissolved organic carbon, and nutrients (Stirling et al., 2020). In contrast, fluctuations in groundwater level stimulate carbon losses (Fenner and Freeman, 2011) and mobilize nutrients (e.g., Meissner et al., 2008).

The exact effect of plant removal on water level depends on the spatial extent and intensity of removal. Within upstream and middle parts of cleared river sections, water levels generally drop immediately after macrophyte removal. At the downstream end of cleared river sections, however, macrophyte removal is unlikely to significantly lower the water level because the impounding effect of dense macrophyte vegetation even further downstream will keep the water level high. Complete prevention of any impounding effect would require the total removal of all macrophytes in a sufficiently long river section. Even if this were possible, the effect of macrophyte removal on water level would only be temporary because the macrophytes regrow. Mechanical macrophyte removal acts as a homogenizing selective force, promoting fast growing macrophyte species (Baattrup-Pedersen et al., 2018). For this reason, macrophyte regrowth may occur within a few weeks to months. In the River Spree, for example, macrophytes have been mowed every summer since 2002, in some years along the whole 34 km river stretch, in others in sections of 3–8 km length. River water levels dropped by 20–30 cm in the mowed sections, but only for some weeks, until regrowth (Jan Köhler, unpublished results).

Removal of macrophytes, therefore, reduces both desired and undesired effects on river flow, and macrophyte removal should aim at balancing desired and undesired effects. Many macrophyte species in temperate rivers die back in autumn, often resulting in a complete lack of macrophytes-related impounding effect from late autumn to spring. In temperate regions, river discharge and the probability of spates are usually lower in summer than in winter/spring. In contrast to solid obstacles like wood or weirs, plants inhabiting lowland rivers are usually flexible and aligned with the flow, reducing drag and impounding effect with increasing flow velocity or discharge (Sand-Jensen, 2003). In such cases, macrophyte removal may reduce an already low flood risk while at the same time removing the positive effects of aquatic vegetation (see above). Partial removal, therefore, might be a compromise (Verschoren et al., 2017). Macrophyte removal restricted to the middle of the river may focus river flow and subsequently increase bed erosion and therefore (possibly undesirable) deepen the channel (Rasmussen et al., 2021). In contrast, macrophyte removal only at the cut bank may favour meandering by causing some bank erosion at the outside and particle deposition at the inside of the meander. This method of macrophyte removal could moderately lower the water level, support a river morphometry closer to natural conditions, and minimize negative effects on biodiversity and on water and particle retention, if the surrounding land use and management regulations permit it.

4.2. Effects of macrophyte removal on nutrient and carbon cycling

High nutrient uptake and allelopathy by macrophytes (Van Donk and Van de Bund, 2002) can reduce the abundance of phytoplankton and cyanobacteria (Deaver et al., 2005; Hilt et al., 2006), promoting clear water conditions. Additionally, dense macrophyte stands filter particles from the water layer and promote sedimentation and carbon burial (Hilt et al., 2017), which further improves light penetration into the water layer. Reduced flow in rivers increases residence time (see Section 4.1), stimulating nutrient uptake by macrophytes and permanent nitrogen removal through coupled nitrification and denitrification by bacteria growing on macrophyte surfaces (Körner, 1999; Beaulieu et al., 2011). At our study sites, we measured water chemistry in control and impact areas (5–6 replicates per site) before, one week after, and six weeks after macrophyte removal (Harpenslager et al., 2022). At several of our case study sites, these before-after-control-impact measurements showed an increase in nutrient concentrations after macrophytes were removed (Table 2). Total phosphorus (P), total organic carbon (TOC), and/or dissolved nitrogen (as NH_4^+) concentrations increased after removal of macrophytes in Lake Grand-Lieu, Lake Kemnade, River Spree and River Otra. The increase in TP, TOC, and NH_4^+ could have resulted from reduced plant uptake or, more likely, from mobilisation from the sediment due to sediment disturbance. Increases in turbidity and suspended particles were observed in multiple study sites after macrophyte removal, which would have resulted from resuspension due to disturbance by mowing activities but may also be caused by reduced particle filtration by macrophytes. The removal of emergent species at Lake Grand-Lieu and River Guaraguaçu impacted physical parameters such as pH, temperature, and DO (Lake Grand-Lieu only), while these parameters were not affected by removal of submerged macrophytes in the rivers Otra and Spree, and in Lake Kemnade (Table 2). At Grand-Lieu, the shallow water layer would have quickly warmed up when shadow by *Ludwigia* was removed, while the most obvious explanation for higher pH and DO would be increased aquatic photosynthesis. Since chlorophyll-a concentrations did not increase after removal of *Ludwigia*, this was not due to free-floating algae, but possibly to filamentous algae or periphyton.

Macrophyte-dominated freshwater systems are often carbon dioxide sinks (Kosten et al., 2012), but sources of methane (CH_4) (Aben et al., 2017). Methane can be released through diffusion, ebullition, or through plant-mediated methane transport. The effect of macrophyte mass developments on fluxes of CH_4 generally depends on the macrophyte life form. Floating macrophytes may form dense surface mats, serving as a barrier to CH_4 ebullition (Kosten et al., 2016), while promoting rhizospheric CH_4 oxidation (Yoshida et al., 2014), thus limiting CH_4 emission to the atmosphere. We measured diffusive fluxes of CO_2 and CH_4 by using closed chambers connected to a portable greenhouse gas analyser, and total daily fluxes of CH_4 by placing closed chambers in the impact and control sites, before and after vegetation removal, and measuring CH_4 in the headspace after 24 h (Harpenslager et al., 2022). Indeed, at Hartbeespoort Dam, we found that removal of floating *Pontederia crassipes* strongly increased CH_4 emission, especially via ebullition (Harpenslager et al., 2022). Plant-mediated methane transport generally is associated with helophytes but has also been reported for submerged or floating macrophytes, including *Ranunculus* spp. (Sanders et al., 2007). Damage by mechanical mowing often results in higher plant-mediated methane emission (Petruzzella et al., 2015). Additionally, sediment disturbance caused by mechanical macrophyte removal could cause mass outgassing of CH_4. This is the most likely explanation for the strong reduction in CH_4 ebullition measured at Lake Kemnade after removal of submerged *Elodea nuttallii* (Harpenslager et al., 2022). The removal of the dominant primary producer would generally also strongly reduce CO_2 fixation and increase CO_2 emission, although effects can be temporary. At Lake Kemnade, for example, CO_2 fixation was reduced immediately after removal of *E. nuttallii*, but macrophyte regrowth quickly returned daytime CO_2 fluxes to levels before removal (Harpenslager et al., 2022).

Generally, macrophyte removal increased nutrient concentrations in the surface water at our study sites, while effects on greenhouse gas emissions differed between sites and plant life forms. Both are at least partially caused by disturbance of the sediment during mowing and may thus be temporary effects.

4.3. Targeted removal of non-native species may not solve the problem of nuisance growth

Non-native macrophyte species may have a competitive advantage over native species because, for example, they are less grazed upon (Keane and Crawley, 2002), use available nutrients in a more effective way (Thiébaut, 2005), tolerate lower light conditions, or have a higher growth rate than native species because they allocate their energy to growth rather than to defence (Blossey and Nötzold, 1995). For these reasons, non-native plants may produce more biomass than do native species with a comparable growth form and life cycle. Non-native

Table 2

Effects of macrophyte removal on physical and chemical parameters of freshwater systems; parameters were quantified in control and impact areas (5–6 replicates per site) before, one week after, and six weeks after macrophyte removal. All measurements and analyses are described in detail in Harpenslager et al., 2022. Two-way ANOVAs were used to determine whether an interactive effect could be found between treatment (impact or control) and time (before or after removal); + depicts an increase, − a decrease, and 0 means that there was no effect of removal on that parameter. Significance levels are indicated with * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$. Further site details are provided in Table 1.

	River Otra (Norway)	River Spree (Germany)[#]	River Guaraguaçu (Brazil)[##]	Lake Kemnade (Germany)	Lake Grand-Lieu (France)	Hartbeespoort Dam (South Africa)
Nuisance species	*Juncus bulbosus*	*Sagittaria sagittifolia*	*Urochloa arrecta*	*Elodea nuttallii*	*Ludwigia grandiflora* and *L. peploides*	*Pontederia crassipes*
pH	0	0	- **	0	+ *	- ***
DO	0	0	0	0	+ ***	0
Water Temperature	0	0	+ ***	0	+ ***	0
Turbidity	- ***	0	0	0	+ *	0
Particles	+ **	0	0	0	0	0
Chl-a	0	0	NA	0	0	NA
Total P	0	0	NA	+ ***	+ **	0
TOC	+ ***	0	NA	- *	0	0
NH_4^+	0	+ *	NA	0	+*	0

[#] In the River Spree, the control section was downstream of the impact site; in all other sites, the control and impact sites were adjacent with a buffer zone between them.

[##] Not all data could be collected from the River Guaraguaçu (Brazil).

macrophyte species may threaten local aquatic biodiversity by resource competition or habitat alteration (Van Donk and Van de Bund, 2002; Stiers and Triest, 2017). This is a good argument for the removal of non-native plants.

Non-native species may expand into new areas by taking advantage of unexplored resources (Elton, 1958; Fleming and Dibble, 2015) and species interactions, e.g., invasional meltdown (Simberloff and Von Holle, 1999). It is therefore often inherently assumed that removal of these plants re-creates an ecosystem with unexplored resources. Experience has shown, however, that the targeted removal of non-native macrophyte species may not solve the problem of perceived nuisance because other native or non-native macrophyte species can colonize the habitat, creating similar problems for the ecosystem users. For example, Khanna et al. (2018) showed displacement of the non-native *Pontederia crassipes* by non-native *Ludwigia* spp. in the Sacramento-San Joaquin Delta in California after radical management. Removal of non-native *Ludwigia* spp. in the River Don in western France led to mass development of two new non-natives on the site, *Egeria densa* Planch. and *Elodea nuttallii* (Gabrielle Thiebaut, unpublished data). At Hartbeespoort Dam, mass development of the non-native free-floating water hyacinth (*P. crassipes*) was controlled biologically, i.e., by releasing insects that specifically target *P. crassipes* while leaving other plant species untouched (Julie Coetzee, unpublished data). We observed, however, the first signs of another non-native free-floating plant species (*Salvinia minima*) taking over when *P. crassipes* cover was reduced. This indicates that the targeted removal of one species may only shift the problem of perceived nuisance growth to another species, rather than solve it, because removal can facilitate the establishment of other species. When targeting removal of non-native macrophyte species, it is therefore important to assess which other species may take over after successful removal and whether these might create similar (or other) problems for users.

4.4. *Effects of macrophyte removal on aquatic biodiversity*

Macrophytes provide a high structural complexity which provides habitat and/or refuge for many other aquatic organisms. Further, macrophytes and periphyton are an important food source for many aquatic organisms. It is therefore no surprise that despite a high variability of results, Hilt et al. (2017) reported a generally higher diversity of phytoplankton, zooplankton, macroinvertebrates, fish, and birds in macrophyte-dominated as compared to phytoplankton-dominated shallow lakes. This study, however, also reported high variability of results so that in some macrophyte-dominated sites, lower biodiversity was observed, or there were no apparent differences (Hilt et al., 2017, and references therein). This might be explained by the occurrence of dense monospecific macrophyte mats, which can repress more diverse native macrophyte vegetation (Stiers et al., 2011), cause biotic homogenization of aquatic communities (Coetzee et al., 2020), and in some cases, lead to anoxic conditions (Bunch et al., 2010) with a subsequent negative impact on aquatic biodiversity. Similar effects were reported in cases where native macrophytes were replaced by non-native macrophyte species, with negative effects on aquatic biodiversity, ecosystem structure, and function (Coetzee et al., 2020; Motitsoe et al., 2022). In our three study lakes (Table 1), we found a generally higher density and taxa richness of zooplankton and macroinvertebrates within dense mats of macrophytes compared with nearby open-water sites, while there were no differences in phytoplankton (Misteli et al., 2022). Given the overall positive impact of dense macrophyte mats described above, we expected the removal of macrophyte mass developments to have a negative impact on aquatic biodiversity. Macrophyte removal eliminates the habitat provided by macrophytes for macroinvertebrates (Thomaz and da Cunha, 2010) and can also directly impact aquatic communities by removing organisms as bycatch together with the macrophytes. In addition, macrophyte removal strongly disturbs the ecosystem, for example by resuspending sediment (e.g., increased turbidity in the River Otra and Lake Grand-Lieu after macrophyte removal; see Table 2) and thereby hindering photosynthesis of phytoplankton, but also via changes in aquatic community composition (Donohue and Garcia Molinos, 2009).

At our study sites, we sampled phytoplankton, zooplankton and macroinvertebrates in sediment (grab samples) and within macrophytes (sweep samples) in control and impact areas (5 replicates per site) before, one week after, and six weeks after macrophyte removal (Misteli et al., 2023). Overall, our results indicated that mechanical macrophyte removal had a negative effect on the diversity of aquatic communities (Misteli et al., 2023). The effect, however, varied among organism groups and study sites. Diversity was generally less impacted by macrophyte removal in rivers than in lakes, possibly because rivers can be quickly recolonized from undisturbed areas upstream (Misteli et al., 2023). In lakes, diversity of zooplankton and macroinvertebrates living within macrophytes was reduced after macrophyte removal, while phytoplankton diversity tended to increase (Misteli et al., 2023), likely due to the decreased competition for light and nutrients improving conditions for phytoplankton (Scheffer, 1990). It is important to note, however, that the increased diversity of phytoplankton is not necessarily a desirable effect, particularly when it is paralleled by biomass increase, leading to a plankton bloom. We also found some indications that fish may benefit from partial removal of macrophyte mass developments (Thiemer et al., 2024).

Overall, diversity of zooplankton and macroinvertebrates was negatively affected by macrophyte removal, while phytoplankton diversity increased. The intensity and direction of these effects, however, varied among organism groups, and among study sites. In addition, the effects on diversity declined quickly, and six weeks after macrophyte removal we detected almost no significant effects (Misteli et al., 2023).

4.5. *Macrophyte removal treats the symptom rather than the cause*

The removal of nuisance macrophytes has shown positive results with respect to socio-economic and ecological aspects of freshwater bodies (Motitsoe et al., 2022). In principle, managing these dense stands should also allow natural communities and ecosystems to recover. However, the positive effects of removal can be short-lived as above-mentioned, with systems subsequently experiencing phytoplankton blooms (Kuiper et al., 2017), secondary plant invasions (see Section 4.3; Pearson et al., 2016; Strange et al., 2018) or, most commonly, regrowth of the targeted plants (Thiemer et al., 2021). When macrophyte mass developments are mechanically removed while environmental conditions remain unchanged, resources (e.g., nutrients, light, space) will become available to other primary producers such as phytoplankton (including cyanobacteria), periphytic algae and plants. Several studies have shown this pattern, both in situ (e.g., Bicudo et al., 2007) and in vitro (e.g., De Tezanos Pinto et al., 2007) and it was no different in our case studies.

Free-floating water hyacinth (*P. crassipes*) in Hartbeespoort Dam in South Africa was previously combated using herbicides (Van Wyk and Van Wilgen, 2002). After spraying water hyacinth biomass, massive blooms of cyanobacteria occurred in Hartbeespoort Dam. We also observed this effect in our mechanical macrophyte removal experiment (Fig. 2; Misteli et al., 2023). The cyanobacterial bloom likely has benefitted from a combination of high nutrient availability, removal of shading that prevails below dense free-floating plants, as well as liberation from potential allelopathic inhibition by water hyacinth. Moreover, turbid waters prevent the growth of submerged plants and periphytic algae, which are competitors of phytoplankton, and high water temperatures promote fast cyanobacterial growth. Currently, water hyacinth mass development in Hartbeespoort Dam is mostly combated by classical biological control, i.e., by releasing host-specific insects that specifically target water hyacinth. Recent observations indicate that another free-floating plant species, *Salvinia minima*, has increased in biomass, while water hyacinth declined (Coetzee et al.,

Fig. 2. In Hartbeespoort dam, South Africa, a cyanobacterial bloom developed in the "impact" site one week after the mechanical removal of water hyacinth. Picture: A. Petruzzella.

2022). The secondary plant invader likely benefits from high water nutrient concentrations, decreased competition with water hyacinth for resources and space, and the fact that the released biocontrol agents specifically target water hyacinth, thereby favouring competing plant species. Furthermore, in Germany, upon experimental removal of submerged Nuttall's waterweed (*Elodea nuttallii*) in Lake Kemnade, we observed an increase in periphytic algal biomass (unpublished data). Periphytic algae generally benefit from high nutrient concentrations, light that transmits deep enough into the water to enable periphyton growth, and the availability of surfaces on which periphyton may grow (e.g., plant parts that remained after partial macrophyte removal). Therefore, habitat conditions determine which group of primary producers is likely to dominate after the removal of macrophytes.

We observed regrowth of the mechanically removed macrophyte species in all sampling sites. Regrowth occurred within a few weeks (Lake Kemnade, Germany, and Guaraguaçu River, Brazil) to a few years (River Otra, Norway). Over many years, mechanical removal generally favours fast-growing or mowing-adapted macrophyte species (Baattrup-Pedersen et al., 2018). This may lead to a change in macrophyte species composition but may not solve the problem of perceived macrophyte nuisance growth. This indicates that if the underlying reasons for the massive macrophyte development are not mitigated, e.g., nutrient enrichment of freshwaters and reduced ecosystem disturbance, rapid plant regrowth or increased growth of periphyton and phytoplankton, including cyanobacteria, commonly occurs after mechanical plant removal.

5. Why do we manage macrophyte mass developments?

Since the causes of macrophyte mass developments (see Section 3) are often difficult to deal with, every year considerable resources are used for macrophyte removal, in spite of the limited long-term effect of mechanical macrophyte removal documented above (Section 4.5; Pieterse and Murphy, 1990; Hussner et al., 2017). As explained earlier, macrophyte removal may serve several purposes. It can intend to prevent flooding of adjacent land (Section 4.1; Boerema et al., 2014; Vereecken et al., 2006) or clogging of hydropower plants (Dugdale et al., 2013), as well as to facilitate irrigation (Armellina et al., 1996), disease control (Bicudo et al., 2007), trade and commerce (Güereña et al., 2015) and recreational activities such as boating, swimming and angling (Thiemer et al., 2023; Verhofstad and Bakker, 2019; see also Section 2). As addressed above, however, macrophyte removal affects structure and function of freshwater ecosystems in various ways, depending on removal intensity (see Section 4). Decision making on macrophyte removal would therefore benefit from integrating the benefits and disbenefits of macrophyte mass development and removal into a consistent framework to guide decision making. The ecosystem services perspective provides such a framework (Mononen et al., 2016; Boerema et al., 2017; Vermaat et al., 2020). Here, we used it to quantify consequences of different macrophyte management scenarios on ecosystem services provisioning (Vermaat et al., 2024).

We used a framework that relates ecosystem functions to 'flows' of final (sensu Boyd and Banzhaf, 2007) ecosystem services and quantified twelve final ecosystem services that are of direct benefit to society (Table 3). These flows were first expressed in biophysical terms and their value to society was then estimated in monetary terms (Vermaat et al., 2024). Expressing flows of ecosystem services in monetary units per unit area and time also allowed us to sum these independent services and estimate Total Economic Value (TEV). Not all services were relevant in each study site. In the River Spree, for example, only nine out of 12 services were relevant (Table 3).

Overall, we found that recreation dominated the estimated TEV of the quantified ecosystem services (Fig. 3; Vermaat et al., 2024). This corresponds with findings elsewhere in the literature where recreation is quantified or where recreation takes place at least to some extent (Vermaat et al., 2016, 2021; Immerzeel et al., 2021). However, often studies only assess some forms of recreation such as angling (e.g., Navrud, 2001; Czajkowski et al., 2015) or bathing (e.g., Lankia et al., 2019), or use non-monetary approaches that preclude the assessment of the relative importance of different services (Burkhard et al., 2009). Recreation is generally hindered when macrophyte stands become so dense that they physically interact with the specific activity or when overall perception of landscape scenic beauty is affected unfavorably. Other than recreation, ecosystem functions that related to final

Table 3
Illustration of the quantification of final ecosystem services in the river Spree for three different management regimes (€ ha-1 y-1; based on Vermaat et al., 2024).

Final service	Derivation	Do nothing	Current	Maximum removal
Provisioning services				
Fodder in the floodplain	Yield statistics on net farmgate revenue from the Federal State of Brandenburg, corrected for the area affected by decreased or increased flooding[*]	111	156	222
Drinking water	Production through bank infiltration in the downstream lake Müggelsee is not affected. Bank infiltration takes only 9 % of the annual flow.	0	0	0
Use of macrophyte biomass for compost production	Not relevant in the river Spree; this has been tested experimentally for the Lake Kemnade but showed to be not cost-effective. In Hartbeespoort Dam a commercial company exploits water hyacinth for the production of compost.	0	0	0
Professional fisheries	Not relevant in the river Spree; for other sites, data were estimated from locally available reports. Professional fisheries with a long history is documented for Lake Grand-Lieu.	0	0	0
Hydropower generation	Not relevant in the river Spree; in the Otra and Lake Kemnade, where hydropower is generated, more or less aquatic vegetation had no measurable effect on hydropower generation. Hartbeespoort Dam is no longer in use for hydropower.	0	0	0
Regulating services				
Clean water for downstream bathing and swimming	Plant mass decaying in autumn forms a load of P to the sediment of downstream lake Müggelsee. This increases the probability of cyanobacterial blooms and reduces the suitability for swimming.	0	0	14
Carbon sequestration	Annual belowground biomass production is buried in the sediment. This is monetized with a low-end shadow market price of 40 € ton C^{-1}.	0.6	0.4	0.1
Cultural services				
Angling	Mean travel distance derived from survey data (Thiemer et al., 2023) and a low-end travel cost separate for residents (5 € per trip) and non-residents (0.22 € km^{-1})	38	42	38
Paddling, boating	Derived from renting company information, revenue multiplied with 0.5 to estimate value corresponding to net farmgate revenue	27	36	45
Swimming, bathing	Similar to angling: survey data, travel distance and travel cost	71	80	71
Appreciation aesthetic scenery	Survey data and tourism statistics for municipalities of Grünheide and Fürstenwalde, passive recreation	414	414	414
Biodiversity non-use	Survey data, fraction of the population with strong affection to nature conservation in the municipalities of Grünheide and Fürstenwalde, published German household willingness to pay for nature conservation (231 €, Boesch et al., 2018). The value is modulated with a multiplier correcting for groundwater level in floodplain nature reserves[*].	100	100	50
SUM	Total Economic Value (TEV)	762	829	854

[*] Whereas increased macrophyte removal reduces flooding of the floodplain and improves productivity of the agricultural land, it also reduces groundwater levels in the floodplain and has a marked negative effect on red-listed plant species in the floodplain wetlands. Flood regulation, thus, is an intermediate service rather than a final service in this case.

ecosystem services were generally found to be little affected (Table 3, Vermaat et al., 2024).

Changing macrophyte removal effort from the current to a more aggressive (economically maximum feasible) removal regime or to a full stop of the removal ('do nothing'), often had surprisingly little effect on the Total Economic Value (Fig. 3; Vermaat et al., 2024). This is illustrated for one case, the River Spree, in Table 3. Only in Hartbeespoort Dam, maximum plant removal led to an increase in TEV, because the value of boating and aesthetic appreciation increased (Fig. 3; Vermaat et al., 2024). In all other cases, maximum removal, despite being costly, had little effect on TEV. In Hartbeespoort Dam and Lake Kemnade, we found a substantial decline in TEV in the 'do nothing' regime, both mainly due to boating (which is no longer possible at high macrophyte densities) and aesthetic appreciation (dense macrophyte stands are often perceived negatively). In the case of the river Spree, we found one distinct trade-off among services: maximum removal led to an increased value of fodder (+40 %) from the agricultural floodplain grasslands (because lower groundwater levels increased productive capacity of the floodplain; see also Section 4.1), but led to a decrease in the value of biodiversity (−50 %) due to the same drop in groundwater levels, leading to the likely decline of red-listed wetland plant species in floodplain nature reserves (Table 3; see also Section 4.1).

All in all, our findings suggest that 'doing nothing' should not be discarded too lightly. Costly removal may not lead to a substantial increase in overall societal value – and it may only benefit a small group of users. Where recreational use is intense, and other, possibly more cause-

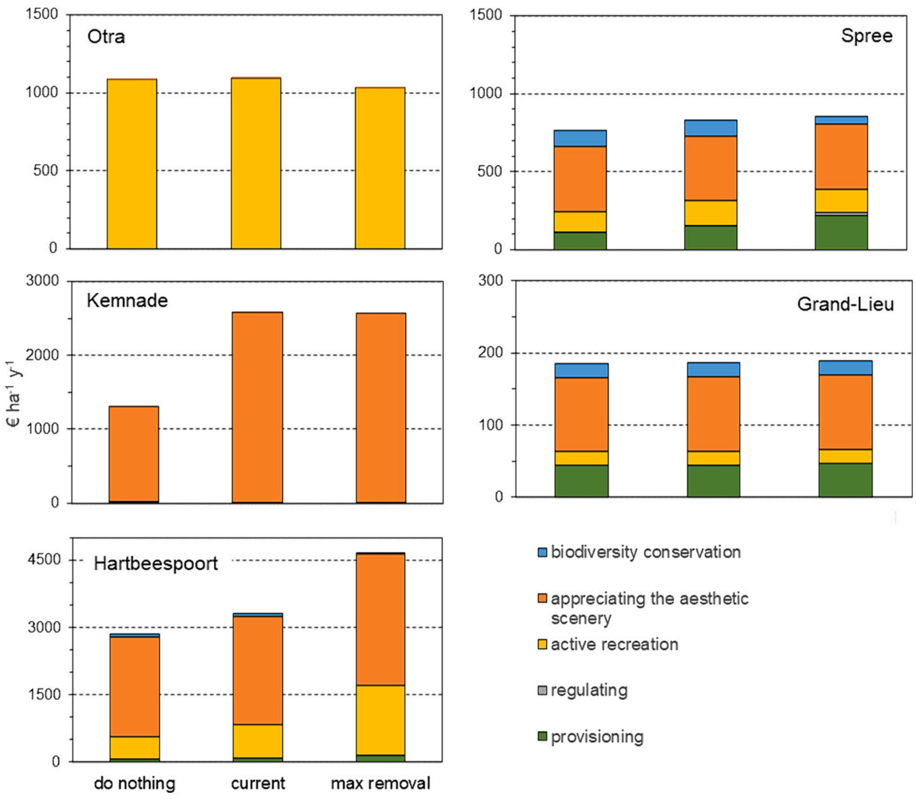

Fig. 3. Effect of management regime (do-nothing, current, and maximum removal) on the monetary value estimate (€ ha − 1 year−1) of different services that add up to total economic value (TEV). Service sequence is the same in all sites, but some services are negligible or absent in some study sites. Based on Vermaat et al. (2024). Mind the different scales on the y-axis.

oriented and biological measures are not feasible, plant removal can be considered. It appears important, however, to weigh aesthetic appreciation by most categories of recreative users against the perceived physical hindrance by a few groups before engaging in costly removal.

6. Lessons learned: Decision support for macrophyte management

Our studies in various freshwater ecosystems (Table 1) support the notion that macrophyte mass development can occur under a broad range of environmental conditions (see Section 3). Macrophyte mass developments can thus potentially become a nuisance for a number of users in almost any water body, while simultaneously facilitating key freshwater ecosystem functions including water provisioning (Section 4.1) and biodiversity habitat (see Section 4.4), as well as nutrient or carbon retention (Section 4.2). Based on our findings, we suggest using a general decision support system before starting macrophyte management in any water body (Fig. 4). The necessary background information for using the decision support system can be collected within the framework of an overall ecosystem services assessment, which may be as worked out as in the example shown in Section 5. It can, however, also be less complex, as long as it clarifies the relevant trade-offs as shown in Fig. 3. The first question (Fig. 4) seems trivial, but our surveys revealed that management decisions are often based only on the needs of a specific subset of users. Secondly, a clear initial definition of the different forms of societal use affected is vital before engaging in macrophyte removal (see Section 2). Thirdly, analysing the reasons for mass development (section 3) offers the chance for more sustainable macrophyte management (C in Fig. 4). Often, however, a limitation of crucial resources (light, nutrients, dissolved inorganic carbon) for macrophyte growth or sufficient natural disturbance preventing macrophyte mass development cannot be reached for various reasons. In such cases, mechanical removal may reduce the perceived hindrance of societal use of the water body. Biological or chemical treatment of macrophyte mass development is possible in some countries (e.g., Coetzee et al., 2020), but is not discussed here, because these options are not always allowed or generally feasible. Costs and efficiency of mechanical removal will differ by region and must be calculated in advance. Although this is usually already done (e.g., Hilt et al., 2006), it also needs to be assessed whether the hindered societal value is more important than the

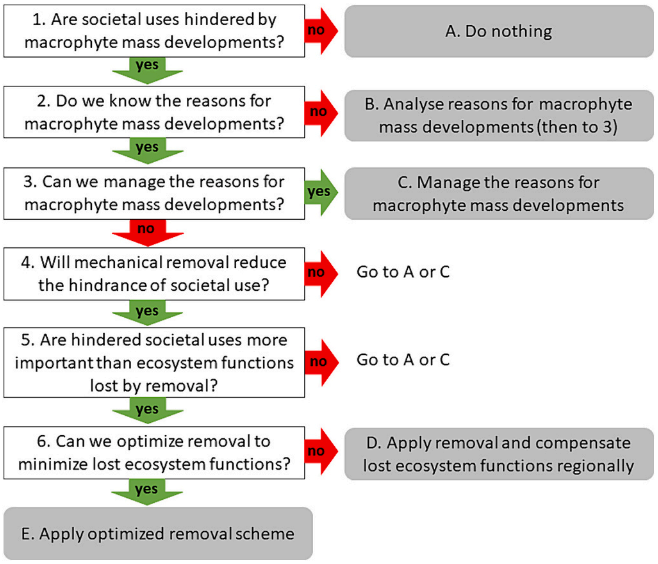

Fig. 4. Decision support scheme for a sound management of macrophyte mass developments.

ecosystem functions lost with macrophyte removal (Fig. 3, see section 4 for an overview on the consequences of macrophyte removal). A spatiotemporally limited macrophyte removal might be considered. However, Van Nes et al. (2002) simulated that realizing a moderate plant biomass by mechanical removal might be the most expensive option or may not be feasible in shallow water bodies. Indeed, our integrating ecosystem services assessment often showed a limited effect of different management regimes on the summed total of societal benefits (Section 5; Vermaat et al., 2024). Alternatively, a compensation of the lost functions could be considered in other water bodies at the regional scale similar to a biodiversity offsetting approach (but see Josefsson et al., 2021). Overall, we suggest that the “do nothing” option should not too easily be discarded in the management of perceived nuisance developments of aquatic plants.

CRediT authorship contribution statement

Susanne C. Schneider: Writing – original draft, Investigation, Funding acquisition, Conceptualization. **Julie A. Coetzee:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Elena Fukasawa Galvanese:** Writing – review & editing, Investigation. **Sarah Faye Harpenslager:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Sabine Hilt:** Writing – review & editing, Investigation, Conceptualization. **Bart Immerzeel:** Writing – review & editing, Validation, Methodology. **Jan Köhler:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Benjamin Misteli:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Samuel N. Motitsoe:** Writing – review & editing, Investigation. **Andre A. Padial:** Writing – review & editing, Funding acquisition, Conceptualization. **Antonella Petruzzella:** Writing – review & editing, Investigation. **Anne Schechner:** Writing – review & editing, Formal analysis. **Gabrielle Thiébaut:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Kirstine Thiemer:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Jan E. Vermaat:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

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Data availability

Data will be made available on request.

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