"MADMACS" – MASS DEVELOPMENT OF AQUATIC MACROPHYTES:

Causes and consequences of macrophyte removal for ecosystem structure, function, and services

Report to the
Water Research Commission

by

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EXECUTIVE SUMMARY

Rationale

Mass development of aquatic macrophytes in rivers and lakes is a global problem, and attempts to remove and control these annually consume substantial sums of money. Aquatic plant removal, however, does not address the causes of the mass development and is not sustainable. In MadMacs we tried to find underlying causes of mass developments of aquatic plants, we studied what exactly happens when the plant masses were removed, and analysed how people perceive the plants. Indeed, mass developments of aquatic plants are generally perceived as problematic, while it is largely unknown that they also deliver several ecosystem services.

Objectives

We aimed to involve key stakeholders into the implementation of our study, and addressed the following questions:

- Which combination of natural conditions and pressures is likely to lead to mass development of macrophytes?
- What are the direct and indirect consequences of macrophyte removal for ecosystem functions and services?
- Which consequences of macrophyte removal are site-specific, and which are general?

The following were the aims of the project:

- to strengthen international collaboration by providing consistent information on causes and consequences of macrophyte mass development across countries
- to set up a model to analyse which combination of natural conditions and stressors can cause mass development of macrophytes
- to set up a model to forecast the consequences of macrophyte removal on aquatic ecosystems
- to quantify the effect of macrophyte presence/removal on structural and functional diversity and abundance of aquatic biota
- to quantify the effect of macrophyte presence/removal on nutrient and carbon retention and removal (water purification)
- to quantify the hydraulic effects of macrophyte presence/removal on adjacent land (impounding, erosion)
- to quantify the effect of macrophyte presence/removal on the full scale of ecosystem services
- to develop a “cookbook”-tool how to assess and balance benefits and dis-benefits of macrophyte removal

In tight collaboration with key stakeholders, we executed a set of “real-world experiments” in a harmonized BACI (Before-After-Control-Impact) design across six case studies in five countries: River Otra in Norway, River Spree and Lake Kemnade in Germany, Lake Grand-Lieu in France, Hartbeespoort Dam in South Africa, and River Guaraguaçu in Brazil. Each of these six sites has experienced mass developments of aquatic macrophytes over the last decades, and the local authorities attempt to control them.

Methodology

In each site, the aquatic plants were removed from a large area (550 m^2 (Lake Grand Lieu) to 70,000 m^2 (River Spree), reflecting current management practices), and the short-term consequences (up to six weeks) of macrophyte removal on biogeochemistry and biodiversity were quantified. Samples of water, plankton, periphyton, plants, macroinvertebrates, fishes and greenhouse gasses (CH_4, CO_2), which are produced in the sediment underneath the plants, were taken. All samples were taken both before and after the plant removal,

in the area where the plants were removed, and in another area where the plants could continue growing. In this way, the consequences plant removal has on the ecosystem were determined. A large survey among local inhabitants and tourists was conducted to determine which group perceives the water plants as problematic, and how important the removal of the aquatic plants is for different user groups. These surveys were announced publicly in newspapers, social media, and info-meetings, through tight collaboration with different local stakeholders and the public. Ecosystem services were quantified, and compared with current management regimes, where the aquatic plants were fully removed, as well as with a "do-nothing" scenario, i.e. where the plants were left standing.

Results

The results from MadMacs were summarised in a set of "key messages"; developed into models to illustrate the causes of macrophyte mass development and the consequences of macrophyte removal; and guidelines were formulated for the management of water courses with dense aquatic vegetation (a cookbook tool). These and other results can be downloaded from https://www.niva.no/en/projectweb/madmacs. Overall, the findings demonstrated that:

- Mass development of macrophytes often occurs in ecosystems which (unintentionally) were turned into a «perfect habitat» for aquatic plants
- Reduced ecosystem disturbance can cause macrophyte mass developments even if nutrient concentrations are low
- Macrophyte removal treats the symptom rather than the cause
- Removal of non-native macrophytes may lead to nuisance growth of other macrophytes
- The effect of macrophyte removal on ecosystem carbon emissions is site-specific
- The consequences of partial macrophyte removal on biodiversity of other organism groups are variable but generally small
- Dense stands of aquatic plants raise the water level of (impound) streams and adjacent groundwater
- Nobody likes macrophyte mass developments, but visitors tend to regard them as less of a nuisance as residents do
- Aquatic plant management often does not affect overall societal value of the ecosystem much

Discussion

MadMacs worked towards a change in attitude of stakeholders (water managers) as well as the general public. Currently, dense macrophyte stands are generally perceived as a nuisance, and managers as well as the general public almost automatically think that dense macrophyte stands must be removed. Therefore, MadMacs's aim was working towards a change in management practice, from "perceived nuisance", towards empirical facts and knowledge-based decision-making, with the understanding that aquatic plants, including dense stands of aquatic plants, in some types of ecosystems are simply a natural occurrence, and that removal therefore can never be sustainable. In the "cookbook", this information is summarized in an understandable way, and guidelines are provided to assess under which circumstances it makes sense to remove macrophytes, and when it does not. "Key messages" from MadMacs have been consolidated, and we actively continue to use this information in the communication with the stakeholders that were involved in MadMacs as well as other stakeholders.

Throughout the project, we collaborated tightly with the stakeholders directly involved in MadMacs, and we received very positive feedback from them. We also established contact with additional relevant stakeholders (e.g. South Africa: the South African Department of Water and Sanitation, Madibeng Municipality, Harties Foundation), discussed and disseminated information on MadMacs and our results via different media channels, including local newspapers, as well as on-site info meetings. Our experiences were very positive, and we genuinely feel that we contributed to an improved understanding of the challenges related to the management of water plants among local and national managers, and the general public.

Having said this, a change in attitude is a long-term process. The challenge of water hyacinth in South Africa, and beyond, must be addressed where the removal of a non-native plant alone may only change the problem but not solve it,

Short Summary Results (Key findings)

While the results of MadMacs highlight the general findings from six case studies, the results from South Africa's case study at Hartbeespoort Dam stood out, largely due to the hypertrophic status of the system, and the nature of water hyacinth invasion. The results show that:

- The construction of Hartbeespoort Dam created a lake with limited flow and extremely high nutrient concentrations from urban waste. Because the water is deep and turbid, few submerged macrophytes grow, but conditions are ideal for the massive growth of free-floating macrophyte species.
- Free-floating water hyacinth in Hartbeespoort Dam was previously combated using herbicides. After spraying water hyacinth biomass, massive blooms of cyanobacteria occurred in Hartbeespoort Dam, an effect which we also observed in our mechanical macrophyte removal experiment. The cyanobacterial bloom likely has benefitted from a combination of high nutrient availability, removal of shading by free-floating aquatic plants, as well as liberation from allelopathic substances which water hyacinth normally releases, turbid water preventing the growth of submerged plants and periphytic algae, and high water temperatures enabling fast cyanobacterial growth.
- Mass development of water hyacinth in Hartbeespoort Dam is currently combated by biocontrol, i.e. by releasing insects that specifically target water hyacinth while leaving other plant species untouched. Recent observations indicate that another free-floating plant species, *Salvinia minima*, has increased in biomass, as water hyacinth declined. The other free-floating plant species 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.
- This indicates that the targeted removal of non-native plant species alone may only shift the problem of perceived nuisance growth to another species, rather than solve it.
- Removal of free-floating water hyacinth in Hartbeespoort Dam strongly increased CH_4 emissions. Likely, the free-floating vegetation before the removal acted as a barrier, which captured CH_4 and stimulated CH_4oxidation in the rhizosphere, thereby oxidising CH_4 that was produced in the anoxic sediment underneath the plants. The removal of the barrier effect resulted in enhanced CH_4 emissions after macrophyte removal. This effect is likely to last until the macrophytes have re-grown.
- No effects of plant removal on diversity and abundance of sediment-dwelling macroinvertebrates were detected in Hartbeespoort Dam (South Africa). This is likely because the removal of free-floating water hyacinth) only slightly disturbed the sediment.

- One week after macrophyte removal, diversity of macroinvertebrates living within macrophyte beds was reduced in Hartbeespoort Dam, but we detected no effect six weeks after macrophyte removal. This indicates that, unsurprisingly, the removal of their habitat affects macroinvertebrates living within macrophytes, but that the remaining and re-growing plants are quickly recolonized.
- In contrast to the other study sites, removal of water hyacinth did not affect the zooplankton living underneath the free-floating plants in Hartbeespoort Dam, while diversity of phytoplankton tended to increase after macrophyte removal. This may be related to the decreased competition for light and nutrients after macrophyte removal, leading to improved conditions for phytoplankton.
- A very high percentage of both visitors and residents (more than 90%) perceived the mass development of water hyacinth as nuisance. People were most concerned about biodiversity, followed by boating and the beauty of the landscape. Hartbeespoort Dam is one of few freshwater bodies which are available for recreation in South Africa, and water hyacinth at this site has been perceived as problematic for decades. The high perception as nuisance, and the absence of a difference between residents and visitors might therefore be related to the fact that people across the entire country have been well aware of the continued struggle against water hyacinth for decades, combined with the high relevance of this water body for the entire country.
- In Hartbeespoort Dam, maximum plant removal would likely increase the estimated total economic value, because the value of boating, angling and passive recreation would increase after plant removal. Mitigating the disadvantage of plant removal (increased risk of toxic cyanobacterial blooms) would cost less than the increase in recreative value. Furthermore, all forms of recreation declined under a do-nothing management regime where water hyacinth cover increases to 50% of the dam's surface, thereby reducing its economic value.

Conclusions

MadMacs combined basic science (ecosystem metabolism) with applied science (macrophyte management) and cross disciplinary science (ecosystem services assessments), and communicated the results in an understandable way to relevant stakeholders, including the public, water managers (e.g. DWS, Water Boards, Local Municipalities) and hydropower companies. MadMacs worked towards a change in attitude of these stakeholders, with the goal to improve the management of water courses with dense aquatic vegetation. Dense macrophyte stands were generally perceived as a nuisance, and managers as well as the general public almost automatically thought that dense macrophyte stands are a sign that something is "wrong" and therefore must be removed.

In conclusion, MadMacs had the following impacts:

- Improved knowledge among water managers, hydropower companies and the public about the underlying causes for macrophyte mass developments. This was achieved through info-meetings and is expected to reach a wider audience in the future due to the publication of the "cookbook" and the MadMacs key messages
- The improved knowledge among the stakeholders enabled a less emotional and instead more informed discussion on the management of macrophyte mass developments, what can and cannot be expected from macrophyte removal, and who must pay for the management

- Stakeholders have started to re-think the sustainability of macrophyte removal. This is an ongoing process. We have not only reached the stakeholders that were directly involved in MadMacs, but also achieved a wider audience (via national meetings with different stakeholders).

Recommendations for further research

In terms of Hartbeespoort Dam management, a ***co-ordinated***, systems approach is needed to manage not only the mass developments, i.e. water hyacinth and now common salvinia, but their cause – the excess nutrient load in the dam. Research needs to focus on how nutrient loads upstream of the Dam can be reduced, as a top priority.

Focus on mass-removal can now rely on the very effective biological control programme against water hyacinth, but an effort into control of common salvinia is needed. However, if nutrient loading is not addressed, the removal of common salvinia will likely result in developments of cyanobacterial blooms which some local stakeholders regard as worse than the water hyacinth mass developments.

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CHAPTER 1: BACKGROUND

1.1 INTRODUCTION

Mass development of aquatic macrophytes (water plants) in rivers and lakes is a worldwide problem. Across the globe, both native and invasive species of macrophytes may exhibit nuisance growth (Hussner et al., 2017). Mass development of macrophytes is generally perceived as a problem, and considerable resources are spent on macrophyte removal (Pieterse & Murphy, 1990; Hussner et al., 2017). However, macrophytes, including very dense stands, also have positive effects on aquatic ecosystems. Among the ecosystem services provided by macrophytes are, for example, nutrient removal and retention (i.e. they contribute to the provision of clean water (UN sustainable development goal (SDG) 6), as well as the provision of habitats for a diverse flora and fauna (i.e. they support life below water; SDG 14, although this presently only is formulated for the sea). Since macrophytes are food and habitat for waterfowl and fish, they contribute to providing a source of protein for low-income riparian subsistence (human) communities. Thus, macrophytes also contribute to SDG 2, no hunger. Macrophytes may also prevent blooms of harmful cyanobacteria (Hilt et al., 2017) and reduce the emissions of greenhouse gases such as methane (Sorrell & Boon, 1992; Kosten et al., 2016). Unfortunately, most ecosystem services provided by macrophytes are largely unknown to the public and water managers. Consequently, management decisions are based on a prevailing negative perception of macrophytes rather than a rational knowledge-based decision. Potential negative consequences of macrophyte removal are generally not considered in management decisions, and follow-up problems often come as a surprise (Hill and Coetzee, 2017). This study, i.e. 'MadMacs' will be the first research initiative to address the multiple and interacting causes leading to macrophyte mass development, which will consistently provide information on both the benefits and costs of macrophyte removal across a wide geographic area.

It is generally assumed that nutrient enrichment is the main driver of macrophyte mass development (Verhofstad et al., 2017). However, this is not always the case (e.g. Moe et al., 2013). In contrast, recovery of water bodies from pollution may also be related to mass developments of macrophytes (Hilt et al., 2011). The specific regional reasons for macrophyte mass development are often poorly understood, likely because it is usually a combination of factors which together cause nuisance growth. This makes analysing causes of nuisance growth at a particular site challenging but relevant. Additionally, there is a lack of replicates, i.e. of standardized before-after-control-impact measurements across several sites. Therefore, results from a particular site have a context-specific component and are difficult to generalize.

Perceived nuisance stands of macrophytes today are either mechanically removed, or chemically or biologically controlled. In Europe, mechanical removal generally is applied, while in South Africa, the US or New Zealand, for example, biological and chemical control also is used. All forms of macrophyte management are costly and have side-effects for the ecosystem. Mechanical removal is often not sustainable because the macrophyte stands generally grow back, and the removal causes other problems to surface (e.g. the mass development of algae or cyanobacteria; Hilt et al., 2017). Biological control may cause follow-up problems (e.g. the mass development of other forms of macrophytes, as presently observed in South Africa; Hill and Coetzee, 2017). Chemical control introduces toxins to aquatic environments, may have yet unknown long-term effects for the environment and therefore, is often disapproved of by the public (Nault et al., 2014). While there exists general descriptions of macrophyte management and control methods, including their effects on the ecosystem (Hussner et al., 2017), there is a lack of quantitative data. Direct costs of the removal of water plants can be relatively easily quantified. Little is known, however, about the indirect costs through the loss of ecosystem services provided by macrophytes. The reasons for this lack of knowledge despite the vast resources spent on macrophyte removal are diverse. Apart from the lack of consistent studies across sites and countries, coordination and understanding between stakeholders responsible for management, and scientists gathering the knowledge, is missing. Such a phenomenon has been observed in other fields (e.g. river restoration; Bernhard et al., 2005).

MadMacs aimed to assess the effects of multiple pressures (e.g. hydromorphological changes, anthropogenic pollution, invasions of non-native species, climate change) on the mass development of macrophytes in freshwater ecosystems, and ecosystem services provided. We assessed the vulnerability and resilience of aquatic ecosystems to multiple pressure factors by analysing which combination of factors is likely to lead to the mass development of macrophytes. We analysed the risks related to multiple pressures by quantifying the direct and indirect costs of macrophyte mass developments. By comparing the costs and benefits of macrophyte removal, we improve the risk-management for degraded ecosystems because water managers will be able to understand and anticipate the consequences of their management decisions. Macrophytes may purify water, i.e. they contribute to the provision of clean water (UN SDG 6). This means they may serve as a low-cost eco-technological solution for the remediation and mitigation of degraded water bodies and aquatic ecosystems.

MadMacs provides consistent and comparable data from five countries across three continents, and thereby contributes to improved management of degraded aquatic ecosystems around the world, as well as to UN SDG 17: partnership for the goals. The results of our project will directly contribute to ensuring a sustainable management of freshwater ecosystems, contribute to clean water, as well as the health and well-being of people that benefit from ecosystem services, and contribute to a sustainable use of water by providing information on the causes of nuisance growth and the consequences of macrophyte removal.

Six case studies, across 5 different countries were conducted to obtain the data required for the study.

***Juncus bulbosus* in the River Otra (Norway)**: mass development of the native macrophyte *J. bulbosus* is the most serious environmental problem in rivers in southern Norway. Annually, on average 250 000 € are spent on abatement measures, but regrowth is generally observed after few years. The Otra River is subject to hydromorphological alterations, climate change and anthropogenic pollution, and the river is used for recreation and hydropower generation.

***Elodea nuttallii* in Lake Müggelsee (Germany):** mass development of the non-native species *E. nuttallii* is a challenge in many water bodies in Germany. In Lake Müggelsee, this species has dramatically increased in abundance. The lake is used intensively for drinking water production, navigation, and recreation, and is subject to climate change, anthropogenic pollution, hydromorphological alterations and an invasion of non-native dreissenid mussels. Risks of mowing *Elodea* have so far not been quantified, but could potentially be serious because a switch to a turbid state could affect drinking water production, especially if cyanobacteria should develop blooms.

***Native macrophytes* in the lower River Spree (Germany):** From the mid-1990s, macrophyte vegetation gradually has increased. In recent years, submerged and floating-leafed macrophytes (mostly *Sagittaria sagittifolia*, *Sparganium emersum* and *Nuphar lutea*) attained a wet weight of 700-800 tons in a 30-km river section, of which about 250-300 t are mechanically removed each year. In parallel with the development of macrophyte biomass, the water level rose by 20-50 cm, causing problems for farmers and residents. Mowing the aquatic vegetation impaired water quality in the downstream river sections and of lakes in the Berlin region. This river section is intensely used for recreation, and the Spree is a main source of drinking water for Berlin.

***Ludwigia* sp. in Lake Grand-Lieu (France):** Lake Grand-Lieu is a large lake with extensive beds of floating-leaved macrophytes. Two non-native aquatic plants (*Ludwigia peploides* and *L. grandiflora*) colonized the lake in the 1990s, developing dense mats in the lake and canals and causing problems for biodiversity conservation and for human activities such as fishing and boating. The lake is affected by eutrophication, climate change, hydromorphological alterations and the invasion of the non-native *Ludwigia* sp. Since 2002, 5-10 tons of *Ludwigia* were removed annually. The management of these invasive species is costly and inefficient, because regrowth is regularly observed, and macrophyte removal reportedly enhanced the development of cyanobacteria in the lake, with negative consequences for fishing and on biodiversity.

***Pontederia crassipes* in Hartbeespoort Dam (South Africa):** Despite efforts to control *P. crassipes*, it remains South Africa's most problematic aquatic macrophyte (Hill and Coetzee, 2017). Hartbeespoort Dam currently is a hotspot of *P. crassipes* invasion. The plant has been present since the 1970s and was successfully controlled in the 1980s using herbicides. In 2016, however, herbicidal control was halted, resulting in massive plant growth. A steering committee has been put in place to draw up a control plan, but this excludes the use of herbicides, which to many seems to be the only viable option. The dam is subject to serious anthropogenic pollution, climate change, and hydromorphological alterations. The primary use of the dam is for irrigation, as well as for domestic and industrial use.

***Urochloa arrecta* in the River Guaraguaçu (Brazil):** *U. arrecta* is an invasive aquatic grass which in the last years produced mass developments in several water bodies in South Brazil. One of these is the River Guaraguaçu, a tidal river. The plant biomass affects the use of the river for navigation, jeopardizes environmental quality for tourism and fisheries, and probably affects the diversity of native species. The River Guaraguaçu is in LAGAMAR, a key region for biodiversity conservation in South Brazil harbouring several endangered species. The river is subject to anthropogenic pollution, climate change, and other invasive species such as catfish which may benefit from the dense *U. arrecta* beds. Management of *U. arrecta* has not yet started, but is under discussion.

The MadMacs case study sites spanned a climatic gradient ranging from an annual average temperature of 4°C (Norway), 8 (Germany), 12 (France), 16 (Brazil) to 20°C (South Africa). This combination enables us to analyse how interactions between natural conditions and pressures lead to undesired mass development of macrophytes

Problem Statement

Problems with macrophyte mass development occur across the world, but managers do not generally exchange experiences across countries, particularly not across continents. Many water managers feel isolated with their particular problem of nuisance growth in their particular system, and their experiences often cannot be compared among each other due to the lack of a harmonized study design. The MadMacs case studies have quite different management histories while at the same time applying a homogenized BACI study design, such that the involved stakeholders and scientists will benefit from the trans-national exchange of experiences. This will generate knowledge which is useful to predict general consequences of macrophyte removal, and will be broadly applicable for management. We will be the first to provide such data, on a trans-national basis, and use them to provide internationally applicable guidelines for a new, knowledge-based management of water courses with dense aquatic vegetation. Among others, we will provide innovative solutions in the sense that the “informed-do-nothing-option”, i.e. not removing macrophyte mass developments, in some (but not all) cases may turn out to be the best option, in addition to being the cheapest. This is indeed ground-breaking, and will be surprising for many.

1.2 PROJECT AIMS

We aimed to involve key stakeholders into the implementation of our study, and addressed the following questions:

- Which combination of natural conditions and pressures is likely to lead to mass development of macrophytes?
- What are the direct and indirect consequences of macrophyte removal for ecosystem functions and services?
- Which consequences of macrophyte removal are site-specific, and which are general?

We aimed to develop a risk assessment model using causal pathway analysis to generally assess the risk that a site subject to multiple pressures will develop macrophyte mass development. Through tight collaboration with stakeholders on the timing and location of macrophyte removal, we were able to apply a homogenized before-after-control-impact (BACI) design across six case study sites in five countries. This enabled us to separate site-specific from general effects of macrophyte presence and removal. We will combine state-of-the-art technical measurements with modern methods in modelling and ecosystem services assessment, and apply them for solving practical problems. To this end, we have developed and disseminate a “cookbook” for the management of water bodies with dense aquatic vegetation. The table below illustrates the objectives of the project.

The following were the aims of the project:

	Statement of Objective
O1	to strengthen international collaboration by providing consistent information on causes and consequences of macrophyte mass development across countries
O2.1	to set up a model to analyse which combination of natural conditions and stressors can cause mass development of macrophytes
O2.2	to set up a model to forecast the consequences of macrophyte removal on aquatic ecosystems
O3.1	to quantify the effect of macrophyte presence/removal on structural and functional diversity and abundance of aquatic biota
O3.2	to quantify the effect of macrophyte presence/removal on nutrient and carbon retention and removal (water purification)
O3.3	to quantify the hydraulic effects of macrophyte presence/removal on adjacent land (impounding, erosion)
O3.4	to quantify the effect of macrophyte presence/removal on the full scale of ecosystem services
O4	to develop a “cookbook”-tool how to assess and balance benefits and dis-benefits of macrophyte removal
O5	to improve the management of water courses with dense aquatic vegetation

1.3 SCOPE AND LIMITATIONS

All milestones were reached, although some were slightly delayed due to the challenges mainly related to the COVID-19 pandemic and the delayed funding of our partner from Brazil. The COVID-19 pandemic prevented the exchange of personnel and equipment among partners during most of 2020 (i.e. including the main field season of MadMacs). We re-organized field work such that most of the samples were taken by the local teams, and later sent to the partners responsible for analyses. However, some of the samples were partly unfrozen at arrival. COVID-19 clearly lead to some delays, because laboratories were closed during the shutdown, causing a back log of samples which later needed to be analysed. In addition, some samples could not be taken because the experts could not travel, and the local scientists could not be trained fast enough to do the sampling on their own.

In addition, the funding agency in Brazil (‘Fundação Araucária’) delayed the start of the financial support. In addition, financial support was also affected by Brazilian governmental regulations that restricted the use of money by federal universities. This caused a mismatch of deadlines among project partners (e.g. PhD thesis needed to be submitted before the data from Brazil were available), such that the data from Brazil could not be included in some of the manuscripts. Overall, however, this did not affect the main conclusions, deliverables and knowledge outputs from MadMacs.

CHAPTER 2: SHORT-TERM EFFECTS OF MACROPHYTE REMOVAL ON AQUATIC BIODIVERSITY IN RIVERS AND LAKES[1]

2.1 INTRODUCTION

Macrophytes play a crucial role in the functioning of aquatic and wetland systems and support a variety of ecosystem services (Hilt et al., 2017; Janssen et al., 2021). Under favourable environmental conditions (e.g. light, temperature, nutrients), exotic and native species can form dense stands within a short time (Riis and Biggs, 2001; Hussner et al., 2017) which can hinder commercial and leisure activities such as navigation, fishing, swimming and other water sports (Dugdale et al., 2013; Güerena et al., 2015; Verhofstad and Bakker, 2019). Furthermore, dense vegetation increases the risk of flood for adjacent land (Boerema et al., 2014), can clog hydropower stations (Dugdale et al., 2013), and represses a more diverse native vegetation (Stiers et al., 2011). Dense mats of floating plants create anoxic conditions (Janse and Van Puijenbroek, 1998). Mass development of macrophytes is thus often perceived as problematic, and managed through physical removal (Hussner et al., 2017; Thiemer et al., 2021), resulting in high financial costs for local authorities and taxpayers (de Winston et al., 2013). As mass developments are expected to increase in the future due to global change, their removal will become more important and balanced management strategies are needed (Hussner et al., 2017; Thiemer et al., 2021). However, studies on the effect of macrophyte removal on aquatic ecosystems are scarce including how this management strategy affects the diversity of phytoplankton, zooplankton and macroinvertebrates (Thiemer et al., 2021).

Macrophyte removal could affect phytoplankton, zooplankton and macroinvertebrate assemblages, with consequences for ecosystem functioning. Macrophytes increase structural complexity and heterogeneity in the water column and offer habitats that would otherwise not be available (Thomaz et al., 2008). Dense macrophyte stands offer space, shelter and a source of food (directly or via epiphytic algae and bacteria) to macroinvertebrates (Ferreiro et al., 2014; Wolters et al., 2019), but they can also reduce the dissolved oxygen availability in the water, negatively affecting macroinvertebrates (Caraco et al., 2006; Stansbury et al., 2008). The effect of macrophytes on zooplankton depends on the interactions with other trophic groups. Studies have shown that zooplankton generally avoids macrophyte beds (Meerhoff et al., 2006), but in the presence of predatory fish, zooplankton use macrophyte beds as a refuge to avoid predation during the day (Burks et al., 2002). Phytoplankton and macrophytes are in direct competition for nutrients and light (Scheffer et al., 1993; Xu et al., 2019). Therefore, the presence of macrophytes hinders the growth of phytoplankton (Van Donk et al., 1993; Scheffer et al., 1993). Besides competition for nutrients, macrophytes have been shown to suppress phytoplankton even under nutrient saturation (Vanderstukken et al., 2011; Amorim and Moura, 2020). The production of allelochemicals by certain macrophyte species also has a strong impact on

[1] Misteli, B., Pannard, A., Aasland, E., Harpenslager, S.F., Motitsoe, S., Thiemer, K., Llopis, S., Coetzee, J., Hilt, S., Köhler, J. and Schneider, S.C., 2023. Short-term effects of macrophyte removal on aquatic biodiversity in rivers and lakes. *Journal of Environmental Management*, *325*, 116442. https://doi.org/10.1016/j.jenvman.2022.116442

phytoplankton (Korner and Nicklisch, 2002; Svanys et al., 2014) especially cyanobacteria, making macrophytes a useful tool in cyanobacteria management (Wang et al., 2012; Bakker and Hilt, 2016).

Studies have shown reduced macroinvertebrate abundance after macrophyte removal in rivers (Kanel et al., 1998; Grygoruk et al., 2015) and lakes (Milisa et al., 2006; Habib and Yousuf, 2014), while others demonstrated neutral (Buczynski et al., 2016; Ward-Campbell et al., 2017) or even positive (Bickel and Closs, 2009) effects, of plant removal on macroinvertebrate abundance. Reduced taxonomic richness was found in a study covering a single river in Australia (Carey et al., 2018), while other studies in lakes and rivers did not find changes in richness (Bickel and Closs, 2009; Ward-Campbell et al., 2017). Shannon diversity was shown to increase in a study in a river in the U.S. (Lusardi et al., 2018), while other studies in rivers did not detect a change in Shannon diversity (Buczynski et al., 2016; Dabkowski et al., 2016). In lakes, several studies reported reduced Shannon diversity (Milisa et al., 2006; Habib and Yousuf, 2014). Depending on the site and its characteristics, the effects are mixed, and it is difficult to detect a general response pattern for macroinvertebrates.

Only few studies are available on the effect of macrophyte removal on zooplankton and phytoplankton. Choi et al. (2014) showed an increase in abundance, richness and diversity of zooplankton after removing free-floating macrophytes in a lake in South Korea. Opposite results for abundance were found in other studies in a Mexican lake (Mangas-Ramírez and Elías-Gutierrez, 2004) and a river in the U.K. (Garner et al., 1996). After plant removal, several studies showed a clear increase in phytoplankton cell density (Wojciechowski et al., 2018) or in Chl-a concentration (James et al., 2002; Bicudo et al., 2007; Kuiper et al., 2017). However, other studies showed a short-term reduction in Chl-a concentration after plant removal (Alam et al., 1996; Morris et al., 2006). Increased turbidity due to the removal likely causes this short-term decrease (Thiemer et al., 2021). Furthermore, the removal of macrophytes increased the abundance of cyanobacteria in tropical lakes (Mangas-Ramírez and Elías-Guti´errez, 2004; Wojciechowski et al., 2018), while Morris et al. (2006) did not find an effect on cyanobacteria in a shallow lake in Australia.

Existing studies on the effect of macrophyte removal on biodiversity often have a narrow scope (e.g. focusing on a single plant species, system or organism group) or a restricted sampling design (e.g. lacking a before-after comparison or a control site). Holistic studies considering multiple groups, species and systems are lacking, but are needed to disentangle general patterns from local differences (Thiemer et al., 2021). Additionally, trait-based analyses, such as functional evenness, functional richness or functional divergence (Villeger et al., 2008), can help to better predict ecological dynamics and increase comparability among different systems (Kremer et al., 2017).

In this study, we analysed the effect of macrophyte removal in three lakes and two rivers with different trophic states (from oligotrophic to hypereutrophic) located in different climate zones (from temperate to tropical climate) along a latitudinal gradient from North Europe to South Africa. At each site, different macrophyte species (native or invasive) are considered problematic, and mechanical removal is part of the current management practice. We applied a BACI design (before-after-control-impact) and sampled macroinvertebrates, zooplankton, and phytoplankton before, and one week and six weeks after plant removal at control and impact sections. Using the same method and the same timespan between macrophyte removal and sampling enables us to compare results among sites. The high variability of our study systems covering different plant types, plant species, trophic levels, system types and climate zones allows us to disentangle general patterns from site-specific effects. We expected to find (i) negative effects of macrophyte removal on macroinvertebrate and zooplankton but positive effects on phytoplankton abundance and diversity; and (ii) strongest impacts on all three groups one week after the removal and a partial recovery six weeks after removal. We applied a comprehensive approach considering six biodiversity and functional indices throughout, using a standardized scoring method.

2.2 METHODS AND MATERIALS

2.2.1 Study locations

We sampled five aquatic systems in four countries in Africa and Europe (Brazil was not included in this study due to COVID-19 delays) (Figure 2.1). The studied systems differed in their physical features, the dominant vegetation and trophic status (Table 2.1). In all sites, dense mats of macrophytes are perceived as problematic and are removed mechanically as part of their management strategy.

The northernmost site was the oligotrophic river Otra in Norway. Our study was conducted in a dammed, slow-flowing part of the river, dominated by the native submerged macrophyte *Juncus bulbosus* L. causing problems for recreational use and hydropower production. Plant stands are usually mowed once every 3 years in early summer. The river Spree (Germany) is characterized by mass development of the native *Sagittaria sagittifolia* L., *Stuckenia pectinata* (L.) Borner and *Nuphar lutea* (L.) Sm. Dense macrophyte stands cause a water level increase of 20-50 cm in summer and increase the risk of flooding adjacent farmland during heavy rainfall events. Mechanical removal is therefore applied once per summer. Lake Kemnade (Kemnader See; Germany) is an important recreational area in a densely populated area. Dense stands of the non-native submerged species *Elodea nuttallii* (Planch.) H.St-John interfere with several recreational activities, and a mowing boat is active daily between May and September. Non-native, amphibious *Ludwigia grandiflora* subsp. *hexapetala* (Hook. & Arn.) G.L. Nesom & Kartesz and *Ludwigia peploides* subsp. *montevidensis* (Spreng.) P.H. Raven dominate in Lake Grand-Lieu (Lac de Grand-Lieu; France), an important nature reserve. The plants have negative effects on native vegetation and human activities such as professional fishing and boating. For 20 years, plants have been removed yearly, which is costly and ineffective due to fast regrowth. In the reservoir Hartbeespoort Dam (South Africa), the floating macrophyte *Pontederia crassipes* Mart. (formerly *Eichhornia crassipes*; Pontederiaceae) covers significant parts of the lake (up to 60%), thereby hindering recreational and commercial activities. In all lakes, we used typical methods used in macrophyte management. All those methods are efficient at removing most of the macrophytes from the treated areas, a small part of the macrophytes, however, will always be left

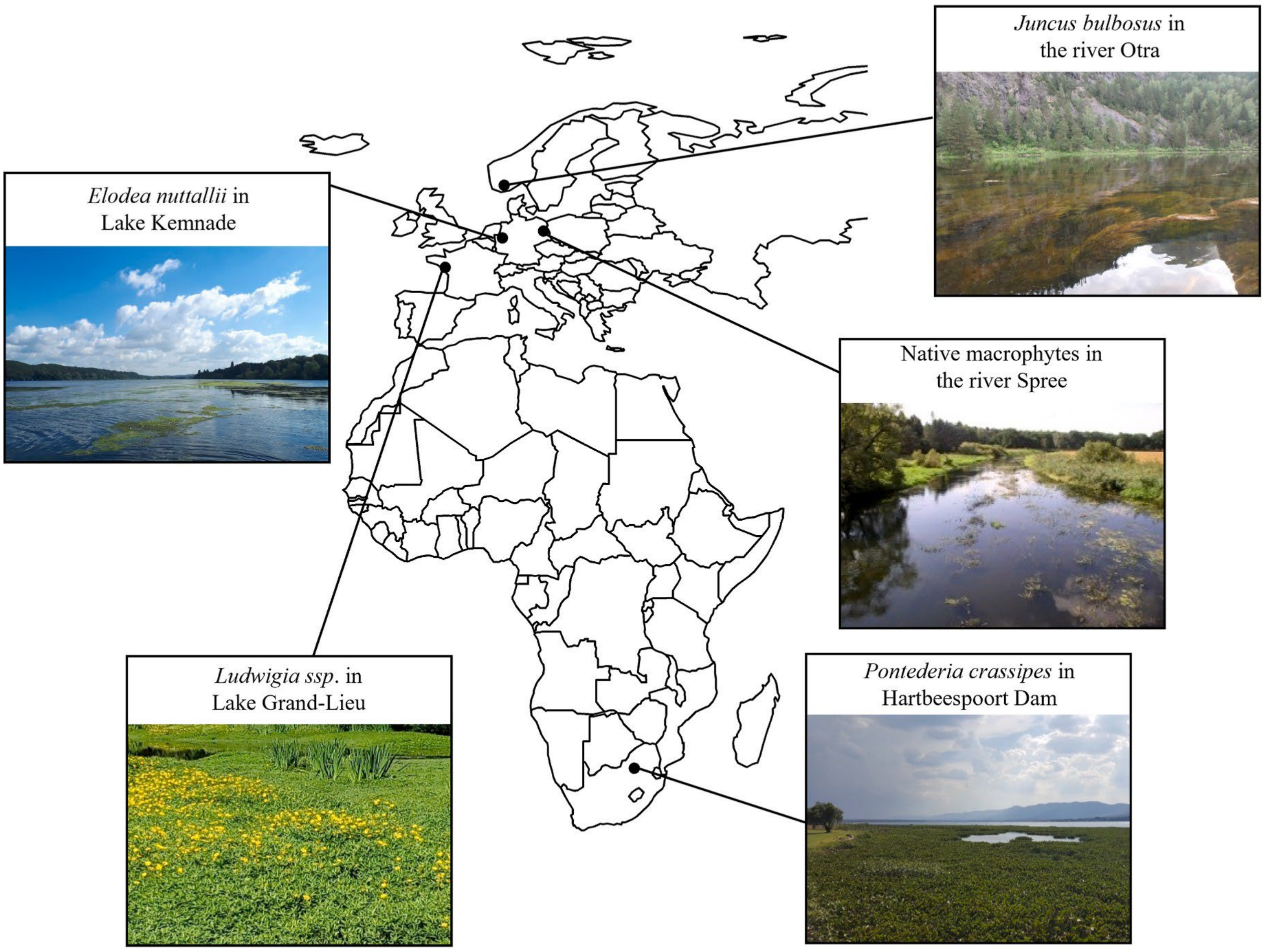


Figure 2.1: Location of the five study systems with mass macrophyte developments.

2.2.2 Study design

Our sampling was performed using a BACI Design (Before-After-Control-Impact (Underwood, 1991),). We defined two sections of comparable size in every study site: one where macrophytes were removed (Impact section) and one where macrophytes were not removed (Control section). In lakes, the two sections were adjacent to each other. In the river Spree, the control section was upstream of the impact section, and in the river Otra, the two sections were located at the opposite shores. Both sections were sampled the week before plants were removed, and then one week and six weeks after plant removal. To reduce sampling bias, both sections were sampled on the same date and by the same people. In every sampling session in each section, five water samples were taken for phytoplankton, five water filtrations were performed for zooplankton, and five grab and sweep samples were taken for macroinvertebrates.

Table 2.1: Site characteristics. Depth and velocity are given for the sampling location. Climate zones according to the Koppen-Geiger classification (Kottek et al., 2006).

Site	Country	Latitude/ Longitude	Water body (size, depth, velocity)	Major problem of mass development	Trophic level	Climate zone	Dominant vegetation	Removal Method	Date of Removal	Size of Impact section
Otra	Norway	59.08864/ 7.550139	Regulated river (depth: 1.5 m, 0.1–0.5 m/s)	Plants hinder boating and fishing and clog the inlet of hydropower plants	Oligo-trophic	Subarctic climate (Dfc)	*Juncus bulbosus (native)*	Mechanical removal with a mowing boat	June 15, 2020–June 22, 2020	33000 m^2
Spree	Germany	52.43076/ 13.678259	River (part of river-lake system, depth: 1.25 m, 0.1 m/s)	Native macrophytes raise water levels and increase the risk of flooding adjacent agricultural land	Eutrophic	Warm-summer humid continental climate(Dfb)	*Sagittaria sagittifolia, Stuckenia pectinata* and *Nuphar lutea (all native)*	Mechanical removal with a mowing boat	10.-17.07.2019 27.–31.07.2020	60000 m^2
Lake Kemnade	Germany	51.41698/- 7.260132	Reservoir (125 ha, depth: 2 m)	Plants hindering sailing and shipping	Eutrophic	Temperate oceanic climate (Cfb)	*Elodea nuttallii (exotic)*	Mechanical removal with a mowing boat	28.-30.07.2020	5000 m^2
Lake Grand-Lieu	France	47.13393/- 1.674355	Shallow lake (64 km^2, depth 1 m)	Non-native macrophytes threatening biodiversity conservation	Hyper-eutrophic	Temperate oceanic climate (Cfb)	*Ludwigia peploides* and *L. grandiflora (both exotic)*	Removal by hand	06.-08.07.2020	550 m^2
Hartbeespoort Dam	South Africa	−25.74929/ 27.833276	Reservoir (2000 ha, depth: 4 m)	Plants causing problems for human lake uses	Hyper-eutrophic	Subtropical highland climate (Cwb)	*Pontederia crassipes* (exotic)	Removal by hand	20.-25.01.2020	625 m^2

2.2.3 Sampling methods and processing

The same sampling method was used in each site and only slightly adjusted to the local conditions.

2.2.3.1 Phytoplankton

°For phytoplankton, sub-surface water samples were taken. According to the expected density of phytoplankton, the volume of sampled water ranged from 50 ml in hypereutrophic sites to 250 ml in oligotrophic sites. Samples were fixed with acidic Lugol's solution and stored in a cold and dark place. All samples were sent to France for identification (Limnologie sarl, Rennes) and counted according to the NF EN 15204 French standard (AFNOR, 2006). Phytoplankton biomass was measured as Chlorophyll-a concentration after filtration on Whatman GF/F glass-fibre filters and extraction with dimethylformamide in a vibration shaker at 4°C. Pigments were separated and quantified by HPLC (see Shatwell et al., 2012 for details).

2.2.3.2 Zooplankton

With a 60 µm mesh, 20-80 ℓ (depending on the characteristics of the system) of surface water per sample were filtered. The sample volume required to collect enough individuals was pre-defined with a test sample, and the same sample size was used for the complete sampling. After filtration, the zooplankton sample was narcotized with carbonated water and then conserved in 80% ethanol and stored at 4°C before identification. Zooplankton was subsampled for identification and identified based on Bledzki and Rybak (2016). Subsamples of a known volume were randomly taken using a Hensen-Stempel pipette and placed in a Bogorov counting chamber. Subsamples were counted until a total of at least 400 organisms were reached. Finally, the abundance was calculated as individuals per litre. In the rivers Otra and Spree, the number of zooplankton collected was low, with many samples being completely empty (mean density of 0.285 individuals per litre in the Spree and 0.031 in the Otra). These sites were therefore excluded from further analysis, and the effect of removal was considered neutral.

2.2.3.3 Macroinvertebrates

For macroinvertebrates, the sampling consisted of grab samples to collect macroinvertebrates associated with the sediment and sweep samples to collect macrophytes associated with the macrophytes. Five grab samples were taken using an Ekman grab sampler, and samples were filtered using a sieve (250 µm mesh size). Five sweep samples were collected using a hand net with a 250 µm mesh size swept harshly through the plants in the case of submerged species, or through the roots for floating species for 30 s over 1 m^2. Both types of samples were stored in 80% ethanol. Macroinvertebrates were separated from sediment under a stereo microscope and identified to the lowest taxonomic level possible.

2.2.4 Biological indices

We used the number of individuals per sample (macroinvertebrates), individuals per litre (zooplankton), and Chl-a concentration (phytoplankton) to quantify abundance of macroinvertebrates, zooplankton, and phytoplankton. Abundance values were log(N+1) transformed for analysis. If individuals were not all identified to the same level, only the lowest identification level was used to estimate taxonomic richness and Shannon diversity to avoid over-estimation. For example, when some individuals were identified to the species level, but others in the same genus could not be identified further, only the species level was included in the analysis.

To assess the functional diversity, we used multidimensional functional diversity indices. A multidimensional space was created with every functional trait representing one dimension, and all taxa and their abundance were plotted in this space. Functional richness (the volume filled by the community of interest), functional evenness (the evenness of abundance distribution) and functional divergence (distribution of the abundance within the volume of the trait space) were used as indices to describe functional diversity (Villeger et al., 2008). Calculations were done with the mFD package in R (Magneville et al., 2022). Due to a lack of precision for available functional information, this analysis was performed at the genus level (or higher taxonomic level if not identified to genus). The following sources were used as a trait database for functional analysis: Tachet et al. (2000) for macroinvertebrates, Gavrilko et al. (2020) for zooplankton, and Padisak et al. (2009) plus Lap-lace-Treyture et al. (2021) for phytoplankton. Used traits are listed in Table S1. Calculating the functional parameters requires at least three taxa, so samples with a lower number of taxa were not analysed. As the composition of the phytoplankton community plays a key role in management strategies, we did an additional analysis of the proportion of the cyanobacteria compared to the complete phytoplankton community based on cell count.

2.2.5 Statistical analysis

All statistical analyses were performed in R version 4.1.2 (R Core Team, 2021). To test the overall effects of plant removal on each parameter across all five systems, linear mixed models (LMM) were performed with the function “lmer” from the package “lme4” (Bates et al., 2015). Statistical parameters for the linear mixed models are summarized in Table S2. “Before-After”, “Control-Impact”, and their interaction were used as fixed factors, and site was included as a random factor (parameter ~ BA * CI + (1|Site)). In addition, each parameter was analyzed separately for each site with two-way ANOVAs using the “aov” function from the package “stats” (R Core Team, 2021). Test statistics can be found in Supplementary Information, Table S3.

2.2.6 Scoring

To summarize and compare the measured effects, we used a scoring system. Every parameter (abundance, taxa richness, Shannon diversity, functional richness, functional evenness, and functional divergence) for every organism group (Zooplankton, Phytoplankton, Macro-invertebrates (Sweep and Grab Samples)) was scored with a value of -1, 0 or +1. If the model (linear mixed models for overall effects and ANOVA for effects by country) showed no significant difference ($p > 0.05$), the score was set to 0. Significant effects were scored with a -1 for a negative impact of macrophyte removal and +1 for positive impacts. The direction of impact was calculated based on the following formula:

$$Effect = (AFTERimpact - AFTERcontrol) - (BEFOREimpact - BEFOREcontrol) \quad [2.1]$$

Percentage differences were calculated based on the "Effect" value above compared to the value in the impact site before removal (BEFOREimpact). Therefore, these values can be lower than -100%. The scoring was done separately for one week and six weeks after sampling. An unweighted scoring together with the presentation of percentage differences were chosen, as the impact on the ecosystem between parameters is not comparable.

2.3 RESULTS

2.3.1 Differences in aquatic biodiversity among sites

Differences in aquatic biodiversity were found between the five sites (Figure 2.2, Figure 2.3). For zooplankton, Lake Grand-Lieu showed the highest abundance with a mean of 4.022 (standard deviation: 0.764) individuals per litre compared to 0.581 (0.133) in Hartbeespoort Dam and 0.178 (0.097) in Lake Kemnade. On the other hand, the zooplankton in Lake Grand-Lieu showed a lower functional richness than the other two sites (0.009 (0.016) compared to 0.175 (0.001) in Lake Kemnade and 0.127 (0.073) in Hartbeespoort Dam). Taxa richness, Shannon diversity, functional evenness and functional divergence were more similar among sites.

For phytoplankton, variations in phytoplankton abundance among sites were high. The three lakes showed higher phytoplankton abundance compared to the rivers, with Hartbeespoort Dam (1330 (562) µg Chl-a/ℓ; only measured one week after the removal in control site) and Lake Grand-Lieu (166 (46) µg Chl-a/ℓ) having the highest estimates, followed by Lake Kemnade (29 (21) µg Chl-a/ℓ), which correlated with the declining order of their trophic status. Phytoplankton abundance was lower in the two rivers, with a higher value in the eutrophic river Spree (4.53 (1.56) µg Chl-a/ℓ) than the oligotrophic river Otra (1.12 (0.03) µg Chl-a/ℓ). As for zooplankton, taxa richness, Shannon diversity, functional richness, functional evenness, and functional divergence did not follow clear trends, and variations were small.

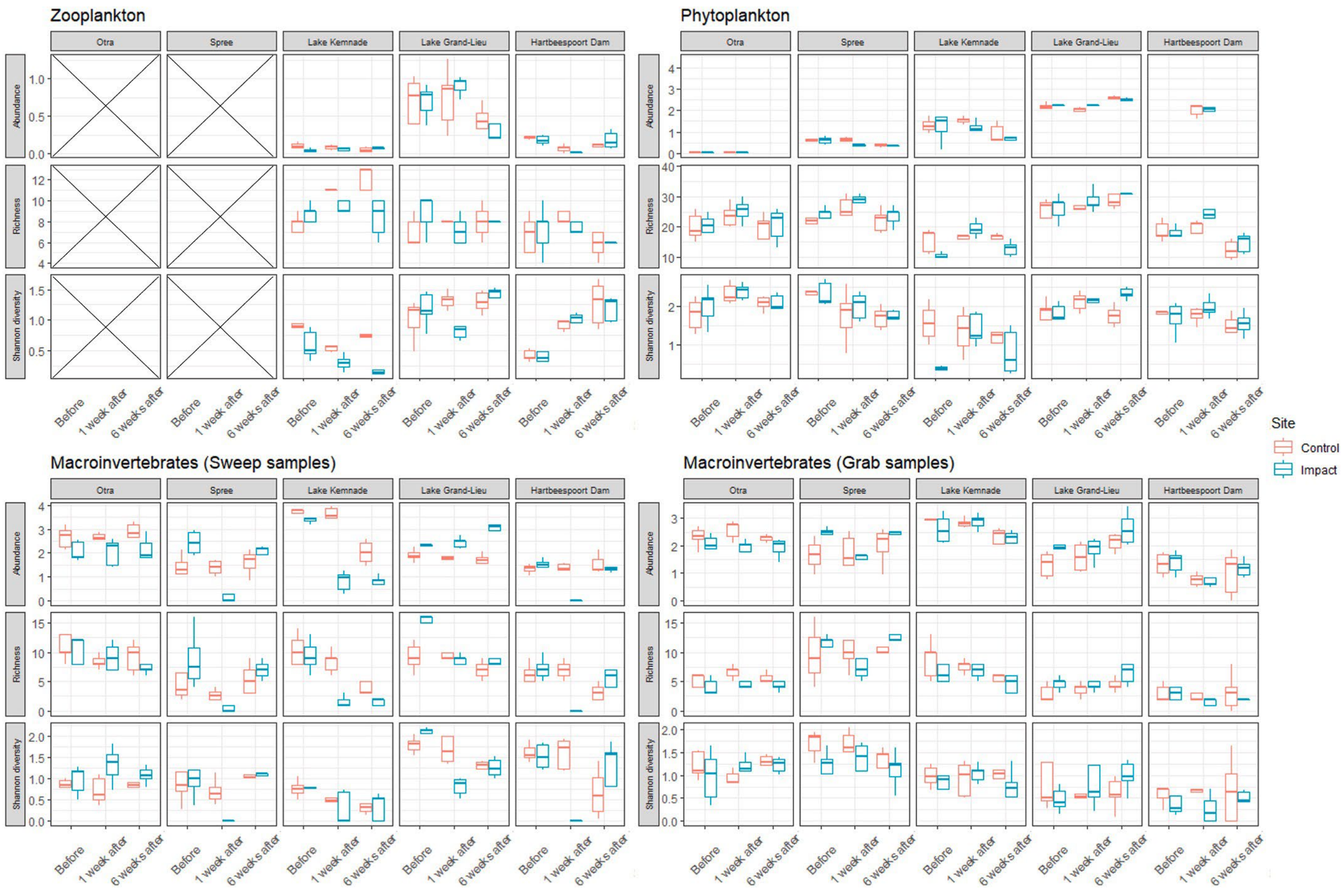


Figure 2.2: Abundance (log+1 transformed), species richness and Shannon diversity of zooplankton, phytoplankton, and macroinvertebrate assemblages from five sites before, one week after, and six weeks after macrophyte removal. Horizontal bold lines represent the median, boxes the 25% and 75% percentiles, and whiskers the minimum and maximum. n = 5 for each sampling time/session.

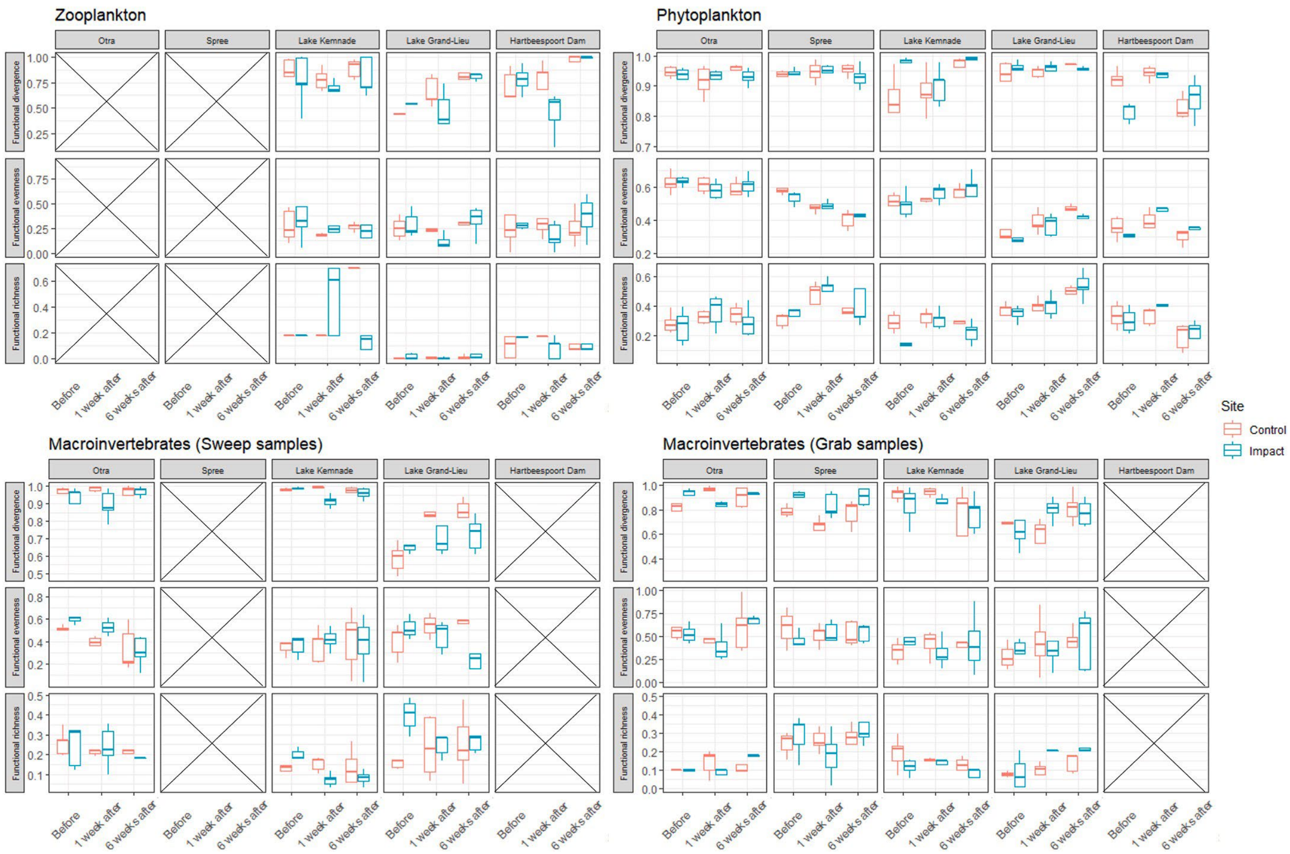


Figure 2.3: Functional divergence, functional evenness and functional Abundance (log+1 transformed), species richness and Shannon diversity of zooplankton, phytoplankton, and macroinvertebrate assemblages from five sites before, one week after, and six weeks after macrophyte removal. Horizontal bold lines represent the median, boxes the 25% and 75% percentiles, and whiskers the minimum and maximum. n = 5 for each sampling time/session

Comparing grab and sweep samples of macroinvertebrates revealed differences in the macroinvertebrate distribution in the five sites. Hartbeespoort Dam (30 (14) individuals per sweep sample; 31 (22) individuals per grab sample) and Lake Grand-Lieu (166 (141); 66 (63)) consistently showed the lowest and second-lowest abundance in both sample types, respectively. For the remaining three sites, Lake Kemnade showed the highest abundance (3837 (1914); 897 (675)). The two rivers showed the second and third highest abundance for sweep samples, Otra (400 (452)) is ranked before Spree (237 (329)) and for the grab samples, Spree (229 (165)) followed by Otra (197 (151)). The taxa richness followed a different pattern than the abundance. For sweep samples, the highest taxa richness was found in Lake Grand-Lieu (12.1 (3.6) taxa found) and for grab samples in Otra (10.4 (2.9)). The lowest taxa richness in both sample types was found in Hartbeespoort Dam (6.8 (1.8) in sweep samples; 3.0 (1.2) in grab samples).

2.3.2 Effects of macrophyte removal on aquatic biodiversity

We found adverse effects of removal on zooplankton assemblage after 1 week as well as six weeks (Table 2.2). In the overall model for one week after the removal, we found a negative impact on taxa richness (-25%; removal effect compared to before sampling in impacted site; see methods) and a negatively impacted functional divergence (-33%). After six weeks, only taxa richness (-25%) was affected in the overall model, while there was no longer an impact on functional divergence. Taking a closer look at each site after one week, we found negative effects only in Lake Grand-Lieu (taxa richness and Shannon diversity), while in Lake Kemnade, we found negative (taxa richness) and positive (functional richness) effects. No effects on zooplankton were found in Hartbeespoort Dam.

Phytoplankton was the only group which was positively impacted by macrophyte removal. The overall model showed a positive effect on taxa richness (17%), Shannon diversity (21%) and functional richness (24%) one week after the removal. After six weeks, the overall model showed no further negative effects. In Lake Kemnade, the river Otra and Hartbeespoort Dam, we found positive effects one week after the removal. After six weeks, only positive effects were found in Hartbeespoort Dam, while in Lake Kemnade, the impact became negative.

Macroinvertebrates associated with macrophytes (sweep samples) were most strongly affected by the removal. After one week, the overall model showed a decrease in abundance (-50%), taxa richness (-49%), Shannon diversity (-48%), functional richness (-48%), and functional divergence (-38%). After six weeks, the overall model no longer showed an impact. The three lake sites were the most strongly affected. While we found some impacts in all three lakes one week after the removal, effects declined over time. We only found a negative impact on the abundance in Lake Kemnade, while we found a positively impacted abundance in Lake Grand-Lieu. The two river sites showed the least effect, and only the abundance was negatively impacted one week after removal in the river Spree, while no impact was found in the river Otra. Macroinvertebrates associated with the sediment (grab samples) were not affected by plant removal in the overall model. Only in the river Otra did we find a negative impact on functional richness (-21%).

We combined all the above-mentioned results in our scoring (-1 for negative effects, +1 for positive effects). Both one-week-after and six-week-after sampling illustrated a negative overall impact of plant removal over all groups with a score of -3 (one-week-after) and -1 (six-week-after). However, no effect was consistent across all sites, and the impacts changed over time with site-specific differences. The strongest negative effect one week after the removal was found in Lake Grand-Lieu (-5) ahead of Hartbeespoort Dam (-2), river Spree (-1) and Lake Kemnade (-1). The river Otra was the only site with positive and negative effects equalizing each other (0). The scores changed strongly after six weeks. Lake Grand-Lieu showed no negative effects. In fact, this site had the highest positive impact, with a score of 2. Hartbeespoort Dam also had a positive score (1), while the two rivers, Otra and Spree, had no effect after six weeks. Lake Kemnade was the only site with a negative score after six weeks (-3).

Table 2.2: Scoring of the impact of macrophyte removal on biodiversity. -1: significant negative effect, 1: significant positive effect, 0: No (significant) effect, 0* = values too low for analysis

		All Site		River Otra		River Spree		Lake Kemnade		Lake Grand-Lieu		Hartbeespoort Dam		Total (parameter)		Total (group)	
	Parameter	**1 week**	**6 weeks**	**1 week**	**6 weeks**	**1 week**	**6 weeks**	**1 week**	**6 weeks**	**1 week**	**6 weeks**	**1 week**	**6 weeks**	**1 week**	**6 weeks**	**1 week**	**6 weeks**
Zooplankton	Abundance	0	0	0*	0*	0*	0*	0	1 (153%)	0	0	0	0	**0**	**1**	**-2**	**-1**
	Richness	-1 (-25%)	-1 (-25%)	0*	0*	0*	0*	-1 (-29%)	-1 (-54%)	-1 (-29%)	0	0	0	**-2**	**-1**		
	Shannon	0	0	0*	0*	0*	0*	0	0	-1 (-59%)	0	0	0	**-1**	**0**		
	F-richness	0	0	0*	0*	0*	0*	1 (169%)	-1 (-266%)	0	0	0	0	**1**	**-1**		
	F-evenness	0	0	0*	0*	0*	0*	0	0	0	0	0	0	**0**	**0**		
	F-divergence	-1 (-33%)	0	0*	0*	0*	0*	0	0	0	0	0	0	**0**	**0**		
Phytoplankton	Abundance	0	0	1 (59%)	NA	0	0	0	0	0	0	NA	NA	**1**	**0**	**5**	**1**
	Richness	1 (17%)	0	0	0	0	0	1 (70%)	0	0	0	0	0	**1**	**0**		
	Shannon	1 (21%)	0	0	0	0	0	1 (332%)	0	0	1 (43%)	0	0	**1**	**1**		
	F-richness	1 (24%)	0	0	0	0	0	1 (105%)	0	0	0	0	0	**1**	**0**		
	F-evenness	0	0	0	0	0	0	0	0	0	0	0	0	**0**	**0**		
	F-divergence	0	0	0	0	0	0	0	-1 (-12%)	0	0	1 (10%)	1 (15%)	**1**	**0**		
Macroinvertebrate Sweep	Abundance	-1 (-50%)	0	0	0	-1 (-86%)	0	-1 (-75%)	-1 (-28%)	0	1 (42%)	-1 (-100%)	0	**-3**	**0**	**-11**	**0**
	Richness	-1 (-49%)	0	0	0	0	0	-1 (-62%)	0	-1 (-47%)	0	-1 (-106%)	0	**-3**	**0**		
	Shannon	-1 (-48%)	0	0	0	0	0	0	0	-1 (-51%)	0	-1 (-99%)	0	**-2**	**0**		
	F-richness	-1 (-38%)	0	0	0	0*	0*	-1 (-65%)	0	-1 (-53%)	0	0*	0*	**-2**	**0**		
	F-evenness	0	0	0	0	0*	0*	0	0	0	0	0*	0*	**0**	**0**		
	F-divergence	0	0	0	0	0*	0*	-1 (-8%)	0	0	0	0*	0*	**-1**	**0**		
Macroinvertebrate Grab	Abundance	0	0	0	0	0	0	0	0	0	0	0	0	**0**	**0**	**-1**	**0**
	Richness	0	0	0	0	0	0	0	0	0	0	0	0	**0**	**0**		
	Shannon	0	0	0	0	0	0	0	0	0	0	0	0	**0**	**0**		
	F-richness	0	0	0	0	0	0	0	0	0	0	0*	0*	**0**	**0**		
	F-evenness	0	0	0	0	0	0	0	0	0	0	0*	0*	**0**	**0**		
	F-divergence	0	0	-1 (-21%)	0	0	0	0	0	0	0	0*	0*	**-1**	**0**		
	Total (sitewise)	**-3**	**-1**	**0**	**0**	**-1**	**0**	**-1**	**-3**	**-5**	**2**	**-2**	**1**				

2.3.3 Cyanobacteria

In addition to the scoring, we analyzed the proportion of cyanobacteria in the phytoplankton community to monitor cyanobacteria blooms after the removal of macrophytes. We found a significant increase of the proportion of cyanobacteria only at Hartbeespoort Dam, with an increase of 45% after one week and 70% after six weeks. This increase in cyanobacteria was also visible during fieldwork as a green and foamy layer on the water. In Lake Kemnade, we found a 62% reduction in the proportion of cyanobacteria after one week and 44% after six weeks. There were no significant changes in the cyanobacteria proportion in any of the other sites.

2.4 DISCUSSION

Our results showed that removal of macrophytes affected the diversity of zooplankton, phytoplankton and macroinvertebrates in freshwater lakes and rivers. Although results differed among locations, we found common patterns. Overall, macrophyte removal had negative effects on the zooplankton and macroinvertebrate community and positive effects on the phytoplankton community. These findings are consistent with our first hypothesis. The effects were most pronounced one week after removal, with decreasing effects six weeks after the removal, confirming our second hypothesis.

Macrophyte removal had a stronger effect on macroinvertebrates living on or between plants than on those living in/on the sediment, as illustrated by different responses of the sweep-sampled and grab-sampled communities. This finding aligns with results reported by Kanel et al. (1998), which show stronger effects of plant removal on species living directly on plants than species living in/on the sediment. While macroinvertebrates living within the plants (sweep samples) were negatively affected one week after macrophyte removal, in four out of five studied sites, negative effects only remained at Lake Kemnade six weeks after removal. The strong negative effects on macroinvertebrates associated with macrophytes immediately after removal could be explained by a high bycatch of macroinvertebrates together with the removed macrophytes (Dawson et al., 1991; Young et al., 2004). Lake Grand Lieu showed positive effects six weeks after the removal. The decrease in water level, as well as sediment disturbance after macrophyte removal might have increased the resuspension of sediment and small benthic invertebrates which we usually collect in grab samples but only in low density in sweep samples. The benthic macroinvertebrate community was only negatively affected in the river Otra. The removal practice in the Otra strongly affects the sediment, compared to the other sites where the removal has a smaller impact, which could explain that the Otra is the only site where we found negative effects on macroinvertebrates living in the sediment. The removal of floating plants was expected to have less impact on biodiversity as they only take up a small part of the water column. However, in Hartbeespoort Dam with floating *P. crassipes*, comparable effects to the sites with other plant types were found. The removal of *P. crassipes* has been shown to strongly alter the water chemistry as it can reduce transparency and oxygen levels and increase nutrient availability drastically leading to lethal ammonia levels, all of which have negative effects on biodiversity (Mangas-Ramírez and Elías-Guti´errez, 2004).

Removal of macrophytes had substantial effects on the zooplankton community. The taxa richness and functional divergence were negatively affected one week after plant removal, and taxa richness stayed reduced even after six weeks. This is in accordance with the higher diversity generally found in macrophyte beds compared to open water, associated with a higher habitat complexity (Kovalenko et al., 2012; Choi et al., 2014). In contrast to macroinvertebrates, no reduction in the abundance of zooplankton was found after macrophyte removal. Lake Kemnade even showed increased zooplankton abundance. The small zooplankton size compared to macroinvertebrates might help them avoid ending up as bycatch of macrophyte removal. Our results cannot confirm earlier studies (Garner et al., 1996; Mangas-Ramírez and Elías-Gutierrez, 2004), which found a negative effect of macrophyte removal on zooplankton abundance. The increase in phytoplankton abundance might positively affect the zooplankton abundance due to higher availability of food.

Contrary to zooplankton and macroinvertebrates, we found positive effects on phytoplankton. The removal of macrophytes increased taxa richness, Shannon diversity and functional richness one week after the plant removal. After six weeks, effects of plant removal on the measured diversity/indices were no longer found compared to the control sites. Other studies have found remarkable changes in Chl-a concentration shortly after plant removal, either positive (James et al., 2002; Bicudo et al., 2007) or negative (Alam et al., 1996; Morris et al., 2006). We could not confirm these results with our study. While short-term adverse effects can be explained by increased turbidity (lower light availability), positive effects can be explained by the decreased competition for light and nutrients. Short-term increase of phytoplankton richness and functional richness could be explained by an overlap of remaining plant-associated species and the newly established open water-associated species directly after the removal. Former studies showed differences in the phytoplankton communities associated with macrophytes and open water sections (Gebrehiwot et al., 2017; Wojciechowski et al., 2018). In Hartbeespoort Dam, the only subtropical site in our study, we found a strong increase of cyanobacteria, aligning with studies with comparable results (Mangas-Ramírez and Elías-Gutierrez, 2004; Wojciechowski et al., 2018). Allelopathic effects of *P. crassipes* could explain such increase (Liu et al., 2015). None of the other sites showed an increase in the cyanobacteria proportion, but in Lake Kemnade, the cyanobacteria proportion decreased. The reduction in cyanobacteria proportion in Lake Kemnade could be the consequence of the increased zooplankton abundance, which was shown earlier to have the potential to control cyanobacteria (Ger et al., 2014; Belfiore et al., 2021). In both Hartbeespoort Dam and Lake Kemnade, the effects were already evident after one week and remained until the sixth week.

While we found strong effects on assemblages one week after plant removal in the overall model, the effects did not persist six weeks later. Only zooplankton taxa richness remained reduced, while all other parameters that changed after the removal showed some resilience, and effects were not present after six weeks. Kanel et al. (1998) showed in a Swiss river that the effect of plant removal on macroinvertebrates fluctuated over time, and after 72 days, overall abundance was still affected. Furthermore, different taxa showed different response patterns. Our study did not last for 72 days, but already after six weeks, most effects had dissipated. We also found strong fluctuations in the values over time. Many existing studies only analyse one time point after the removal (e.g. Bickel and Closs, 2009: sampling after four months; Habib and Yousuf, 2014: sampling after 1-5 days), and such timing differences, to some extent, contribute to the different findings in these studies. In many cases, macrophytes regrow after removal (Bickel and Closs, 2009; Thiemer et al., 2021), which might aid recovery of communities. If frequent macrophyte removal is performed, this might hinder the development of a well-adapted community to both the macrophyte and clear water state.

Impacts of plant removal on the aquatic communities were system-specific, even though an overall negative effect across systems was reported. The two least impacted sites were the two rivers. Fast recolonization via drift might help the communities to recover quickly (Walks, 2007; Baxter et al., 2017). The two river sites were the only sites where native vegetation grew in dense mats. Therefore, the effects of removal of native compared to exotic plants cannot be separated from the effects of system type. As different plant growth forms have different effects on other organisms (Walker et al., 2013), we could expect different effects of plant removal depending on the growth form and other plant characteristics (e.g. growth rate, dispersal ability, structural density). However, we could not identify such differences in our study. Another confounding factor in our study was the different ongoing macrophyte management strategies in our systems. All our sites were already managed prior to the experiment, and long-term effects of macrophyte removal in the past years could have affected our outcomes.

The monitoring of environmental impacts depends heavily on the choice of the proper experimental design. A simplified study design often results in an inaccurate estimate of the ecological response (Christie et al., 2019). The choice of a BACI (Before-After-Control-Impact) design turned out to be a good decision for our purpose. Values differed in the two sections already before the plants were removed, even if we chose two nearby sections as control and impact sections. Including a control, site was important as we found high temporal variability in the control site without plant removal. Using only a CI (Control-Impact) or a BA (Before-After) design, as was often the case in former studies, might lead to wrong conclusions, and effects might be overlooked.

While dense mats of macrophytes are often considered a nuisance due to their interference with human lake and river uses, their removal comes with adverse side effects for the ecosystem, including biodiversity. Biodiversity loss, especially in freshwater systems, is one of the biggest challenges of our time (Tickner et al., 2020) and saving biodiversity is part of the sustainable development goals defined by the United Nations (2015). A fact-based, unbiased understanding of macrophytes and their interaction with other organisms is key to developing management strategies to tackle this biodiversity loss. Future sustainable management strategies for mass develop of macrophytes must consider not only the macrophytes as a problem but also other ecosystem services provided such as their role in promoting biodiversity.

CHAPTER 3: SHORT-TERM EFFECTS OF MACROPHYTE REMOVAL ON EMISSION OF CO_2 AND CH_4 IN SHALLOW LAKES[2]

3.1 INTRODUCTION

Mass developments of macrophytes frequently occur in freshwater ecosystems (Hussner et al., 2017). These mass developments not only hinder human recreational activities such as boating or swimming (Verhofstad and Bakker, 2019), but may also increase the risk of flooding of adjacent land (Boerema et al., 2014) and strongly reduce vegetation diversity (Hilt et al., 2006). Therefore, considerable resources are spent on their removal, using either chemical, biological or mechanical approaches (Hussner et al., 2017).

Although mass developments are generally monocultures that may have replaced or threaten a more diverse vegetation, they are still likely to fulfil important functions within the ecosystem. High nutrient uptake by aquatic macrophytes and their periphyton – and in some cases allelopathy – reduces the abundance of phytoplankton (Van Donk and Van de Bund, 2002), creating clear water conditions. Dense macrophyte stands also promote sedimentation and carbon burial (Hilt et al., 2017), thus contributing further to water clarity. Increased surface area for biofilm growth ensures higher nitrogen (N) removal through coupled nitrification and denitrification by the associated microbial community (Korner, 1999). The high surface to volume ratio of submerged macrophytes provides a large surface area for periphyton, while radial oxygen loss from rooted macrophytes can influence the sediment microbiota. This microbial community also uses root exudates and decomposing plant biomass as important sources of organic carbon and nutrients for biogeochemical reactions. Furthermore, macrophyte stands provide both shelter and food to many macroinvertebrates and fish species and support high biodiversity (Hilt et al., 2017).

In freshwater ecosystems with dense aquatic vegetation, macrophytes are expected to have a strong impact on the carbon (C) cycle (Reitsema et al., 2018). Mechanical removal of macrophytes, a common management practice in shallow lakes with dense aquatic vegetation, could therefore affect the fluxes of carbon dioxide (CO_2) and methane (CH_4) in the ecosystem. Macrophyte dominated lakes are often sinks for CO_2 (Kosten et al., 2012). Macrophyte removal could therefore increase CO_2 emission due to reduced primary production, possibly turning the lake into a net source of CO_2. The effect on CH_4 emission seems less straightforward and may depend on macrophyte life form. Rooted macrophytes can oxygenize the sediment, thereby reducing methanogenesis and promoting methane oxidation (Laanbroek, 2010). Their roots may, however, also form a direct pathway for CH_4 emission (via the so-called chimney effect; Bhullar et al., 2013). In systems dominated by dense mats of floating aquatic macrophytes, on the other hand, the

[2] Harpenslager, S.F., Thiemer, K., Levertz, C., Misteli, B., Sebola, K.M., Schneider, S.C., Hilt, S. and Köhler, J., 2022. Short-term effects of macrophyte removal on emission of CO_2 and CH_4 in shallow lakes. *Aquatic Botany*, *182*, 103555. https://doi.org/10.1016/j.aquabot.2022.103555

gas exchange across the water-atmosphere interface is strongly reduced (Attermeyer et al., 2016). While this reduces the oxygen availability in the water column (Morris and Barker, 1977), thereby creating ideal conditions for methanogenesis, the release of this CH_4 may be reduced as floating leaves can 'capture' the gas bubbles (Kosten et al., 2016), while radial oxygen loss may promote CH_4 oxidation (Yoshida et al., 2014). During removal of floating vegetation, sudden release of accumulated CH_4 bubbles may therefore be expected.

A recent review by Thiemer et al. (2021) suggests that mechanical macrophyte removal can have severe negative impacts on ecosystem functioning and structure. Studies on the influence of mechanical macrophyte removal on greenhouse gas emissions, however, are lacking. In this study, we determined the short-term effects of macrophyte removal on fluxes of CO_2 and CH_4 in three shallow lakes infested with invasive macrophytes using a Before-After-Control-Impact (BACI) design. The three lakes were each dominated by macrophytes with a different life form: floating *Pontederia crassipes* (Mart.) in Hartbeespoort Dam (South Africa), submerged *Elodea nuttallii* ((Planch.) St. John) in Lake Kemnade (Germany) and a mix of emergent *Ludwigia grandiflora* and *L. peploides* at Lake Grand-Lieu (France). For each lake, we analysed the effect of macrophyte removal and local environmental conditions on the fluxes of CO_2 and CH_4. We hypothesised that net carbon emission will increase following removal and that the margin of effect will be different between lakes. In addition, we expect that removal of floating vegetation results in a stronger increase in CH_4 emission than that of submerged or emergent plants. Determining these short-term effects will be an important start to understanding how the common management practice of macrophyte removal impacts C-fluxes and ecosystem functioning in freshwater systems.

3.2 MATERIAL AND METHODS

3.2.1 Studied lakes

Three lakes or reservoirs with mass developments of invasive macrophytes were used as case studies (Figure 3.1). Hypertrophic reservoir Hartbeespoort Dam (-25° 44' 30.59"N, 27◦ 52' 0.59" E; area: 1850 ha; mean depth: 9 m) in South Africa has been infested by the floating macrophyte *Pontederia crassipes* (formerly known as *Eichhornia crassipes*) since the 1960s. It is considered a nuisance for recreational activities such as boating. Approximately 10% of *P. crassipes* is removed manually each year on private initiatives along the shoreline. Additionally, biological control has been used since the early 1990s with the following arthropods being introduced: *Neochetina eichhorniae, N bruchi, Eccritotarsus catarinensis, Niphograpta albiguttalis and Orthogalumna terebrantis* (Coetzee et al., 2021). The introduction of *Megamelus scutellaris* in 2018 was followed by a reduction in cover from 47% to 5% in the summer of 2019-2020 (Coetzee et al., 2021). Lake Grand-Lieu in France (47◦ 04' 60.00" N, 1◦ 39' 59.99" E) is a 3500 ha (6300 ha in winter) shallow lake (mean depth 0.7 m and 1.6 m in summer and winter, respectively), which is a protected bird habitat and natural reserve. The lake and its surrounding area have been invaded by two species of the emergent genus *Ludwigia (L. grandiflora subsp. hexapetala* (Hook. & Arn.) G.L. Nesom & Kartesz and *L. peploides* subsp.

montevidensis (Spreng.) P.H. Raven) since the 1990s. To reduce the impact on native vegetation, *Ludwigia* is manually removed every year (2020: 64 m^2; (Pierre, 2020)). Lake Kemnade in Germany (51◦ 25’ 13.825" N 7◦ 15’ 41.674" E) is a reservoir in the river Ruhr, with a surface area of 125 ha and a mean depth of 2.4 m. Since the early 2000s, the reservoirs in this area have seen mass development of *Elodea nuttallii*, an invasive submerged macrophyte that severely impacts recreational activities (boating, fishing, swimming) in the lake. At Lake Kemnade, *E. nuttallii* is removed annually using a specialised mowing boat, which is continuously deployed by the local water authorities between May and September. During 2020, approximately 1500 m^3 of *E. nuttallii* was removed from the lake (Ruhrverband, 2020). To prevent damage to this mowing boat, the bottom 50 cm of the lake are not mowed, thus leaving part of the mass development behind.

3.2.2 Experimental design

Our sampling of the three lakes was carried out in the summer of 2020 (Jan-March in South Africa; June-August in Europe), using a standardised BACI design. In each location, two plots were created in a section of the lake with homogenous, dense vegetation. In one of these plots, macrophytes were removed either mechanically or manually (impact site). Meanwhile, a similarly sized plot, located at approximately 5 m, 100 m and 30 m from the impact plot at Hartbeespoort Dam, Lake Kemnade and Lake Grand-Lieu, respectively, was assigned as a vegetated control (control site) (Figure 3.1). Plot size differed between lakes, reflecting the current management practices. Plots measured 625 (depth 1.2-1.8 m), 5000 (depth 1.3-1.5 m) and 500-550 m^2 (depth 0.3-0.5 m) for Hartbeespoort Dam, Lake Kemnade and Lake Grand-Lieu, respectively. Removal took place over 2-3 days. Fluxes of CO_2 and CH_4 and environmental conditions were measured one week before and one week after macrophyte removal. Additional measurements were conducted during the 24 h immediately after removal (to determine the disturbance effects) and six weeks after removal.

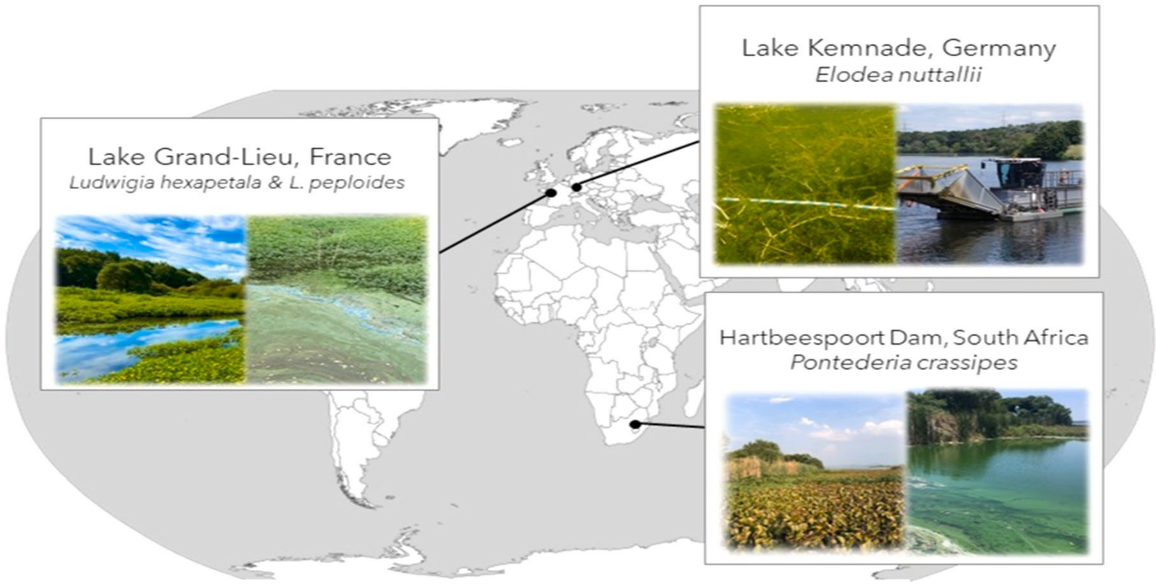


Figure 3.1: Map indicating the locations of the three lakes with mass developments of invasive macrophytes. After removal of both *Ludwigia* spp. (Lake Grand-Lieu) and *P. crassipes* (Hartbeespoort Dam), blooms of cyanobacteria occurred. At Lake Kemnade, a specialised mowing boat was used to remove *E. nuttallii* throughout the summer months.

3.2.3 Emission of methane and carbon dioxide

Diffusive fluxes of CO_2 and CH_4 (including plant-mediated CH_4 transport) were determined in-situ in Lake Kemnade and Hartbeespoort Dam, using an opaque, closed chamber connected to a portable green-house gas analyser (LGR-MGGA; cavity enhanced absorption greenhouse gas analyser; Los Gatos Research-ICOS, U.S.A.). Opaque rather than transparent chambers were used to avoid problems with condensation at the relatively high ambient temperatures at our lakes. While photosynthetic activity of submerged *E. nuttallii* could be approximated with this method, carbon uptake by floating *P. crassipes* could have been underestimated as its uptake of atmospheric CO_2 would be limited by shading. Diffusive fluxes could not be measured at Lake Grand-Lieu due to COVID-19 travel restrictions. Chambers had circular bases with a diameter of 40 and 30 cm and total volumes of 16 and 24 ℓ at Lake Kemnade and Hartbeespoort Dam, respectively. Due to low water flow in Lake Kemnade, the closed chambers were not anchored and therefore free to drift next to the boat as recommended by Lorke et al. (2015). In Hartbeespoort Dam, dense cover of *P. crassipes* prevented the chambers to drift. Each chamber was therefore carefully placed over a *P. crassipes* plant and allowed to equilibrate for 10 min before connecting the GHG analyser. Chambers were aired between measurements. Measurements were repeated in 3-4 locations within the impact and the control site, and repeated multiple times a day (generally early morning, noon and late afternoon), and 1-3 times in each period (before, immediately after and one and six weeks after removal). During measurements, chambers were kept on until a clear ($R^2 > 0.9$) linear increase had been observed for approximately 5 min. The linear increase of CO_2 and CH_4 concentrations inside the chamber (in ppm) were then converted to diffusive fluxes per m^2 using the following formula

$$F_{dif} = \frac{\Delta C_i}{\Delta t} * \frac{P}{R^*T} * M * \frac{V_i}{A_i} * 1000 \qquad [3.1]$$

in which F_{dif} is the diffusive flux (mg C m^{-2} h^{-1}), ΔC/Δt is the change in CH_4 or CO_2 concentration (in ppm • 10^{-6}) in the headspace of chamber i over time (h), P is atmospheric pressure (in atm.), R is the gas constant (L* atm / mol * K), T is temperature (K), M is the molar mass of carbon (g mol^{-1}) and Vi (L) and Ai (m^2) are the volume and area of chamber i, respectively.

Total daily fluxes of CH_4 (including diffusion, ebullition and plant-mediated CH_4 transport) were determined at all lakes by placing opaque closed chambers (n = 4 at Lake Grand-Lieu and Hartbeespoort Dam; n = 5 at Lake Kemnade; same dimensions as described above) in the impact and control sites, before and after vegetation removal. Chambers rather than commonly used funnels (but see (Cole et al., 2010; Peixoto et al., 2016)) were used to be able to cover the vegetation, and thus include plant-mediated CH_4 transport. Since some emergent species switch from convective to diffusive gas transport during dark periods (Chanton et al., 1993), using opaque chambers may have underestimated plant-mediated CH_4 transport by *Ludwigia*, although Brix et al. (1992) could not detect convective flow in *Ludwigia peploides*. Chambers were placed with open valves for 30 min to equilibrate before a background sample was collected. Valves were then closed, and after 24 h, a final headspace sample was collected. Before sampling, a 30 mL syringe was used to flush the headspace several times to ensure mixing before the actual sample was collected. The headspace samples were transferred into 3 mL gastight vials with a septum lid (Labco, High Wycombe, UK), by displacing a known amount of demineralised water from the vial. Samples were stored upside down to prevent leaking and were analysed by injection into the portable greenhouse gas analyser (described above). For this, a closed loop was created by connecting the inlet and outlet of the analyser by gastight tubing with a glass injection port in between. Samples were collected with a glass gastight syringe (Hamilton 250 µL RN syringe with 26 G removable needle) and injected into the custom-build injection port through a 12.7 mm septum (premium-non-stick BTO septum, Restek), which was replaced after every 50 samples. Samples collected at Lake Kemnade and Hartbeespoort Dam were analysed on-site within one week, while samples collected at Lake Grand-Lieu were analysed after approximately 1 month. Total CH_4 emission rates were calculated with the following formula:

$$F_{tot} = \left(\frac{C_{i,\,24} - C_{i,\,0}}{\Delta t} * \frac{P}{R*T} * M * \frac{V_i}{A_i} * 1000\right) + (k*(\overline{C}_h - C_w)*\alpha) \qquad [3.2]$$

where F_{tot} is the total flux of CH_4 emitted to the atmosphere (mg CH_4-Cm-2 h-1), Ci, 24 and Ci,0 are the concentrations (ppm •10-6) of CH_4 in the headspace of chamber i at 24 and 0 h, respectively, Δ t is the exact time that the chamber was deployed (approx. 24 h), P is atmospheric pressure (atm.), R is the gas constant (L * atm / mol * K), T is temperature (K), M is the molar mass of carbon (g mol^{-1}) and Vi (l) and Ai (m^2) are the volume and area of chamber i, respectively.

Fluxes were excluded (8 out of 123 measurements) when obvious disturbance had been noted in the field (e.g. chambers were not sealed properly on return). When headspace CH_4 concentrations in the floating chambers exceeded concentrations in the water layer, CH_4 may diffuse back into the water layer. The second term of Eq. 2 therefore applies a correction to account for the potential underestimation of the total fluxes (similar approach to (Oliveira-Junior et al., 2018), where k is the gas transfer velocity (set to 0.05 m d-1 as wind impact was strongly reduced within the floating chamber), Ch is the average CH_4 concentration in the headspace of the chamber and Cw is the dissolved CH_4 concentration in the water. The dissolved CH_4 concentration in the water (Cw) was determined in water samples that were collected separately by carefully filling 3 mL gastight vials completely with lake water before the start of the total flux measurements. After displacing 1 mL of water with N_2 gas and equilibrating, the CH_4 concentration in the headspace was measured by injecting into the inlet port in the MGGA greenhouse gas analyser as described above, after which, the Bunsen coefficient (using the formula and constants from Yamamoto et al. (1976) at ambient temperature in K) was used to determine the dissolved CH_4 concentration. The loss of CH_4 by diffusion from the headspace into the water layer made up approximately 15%, 23% and 11% of the total CH_4 flux at Lake Grand Lieu, Lake Kemnade and Hartbeespoort Dam, respectively. Finally, we estimated the contribution of ebullition to the total CH_4 emission from Lake Kemnade and Hartbeespoort Dam, by subtracting diffusive fluxes from total fluxes (assuming both fluxes included plant-mediated methane transport).

3.2.4 Dissolved CH_4 in the rhizosphere of *P. crassipes*

At Hartbeespoort Dam, acrylic dialysis chambers (Hesslein, 1976) with 20 equally spaced 10 mL sampling ports (one port per cm depth), were filled with demineralised water and closed off with a HT-Tuffryn 200 membrane (0.45 µm; GELMAN). The frames were installed just below the water surface at the impact and control sites and left for 24 h (before and after macrophyte removal), to allow equilibration of the concentrations of nutrients and elements across the membrane into the demineralised water. Samples were collected from sampling ports at 1, 6, 11, 16 and 20 cm depth by careful pipetting and transferred to gastight vials (filled completely and fixed with 15 µL 50% $ZnCl_2$) for analyses of dissolved CH_4 concentrations (as described above).

3.2.5 Potential methane production

At Lake Kemnade and Hartbeespoort Dam, sediment incubations were carried out to determine potential CH_4 production rates of the sediment. For this, sediment was collected from the upper sediment layer (0-10 cm depth) and mixed, before being added to glass bottles (1 ℓ DURAN GL 45 with bromobutyl rubber stoppers (DWK) at Lake Kemnade and 22 mL amber glass screwtop vials (Labsolute) fitted with magnetic screw caps with PTFE-sillicone septa (18 mm; 10 mil; Restek) at Hartbeespoort Dam). Bottles were incubated in the dark, at 20°C at Lake Kemnade and 30°C at Hartbeespoort Dam to reflect ambient temperature. Incubations were carried out with 150 mL and 15 mL sediment at Lake Kemnade and Hartbeespoort Dam, respectively. Bottles were filled with filtered (0.7 µm) lake water, leaving a headspace of 105 and 4 mL respectively (approximately 10-20% in both experiments, which should minimise a lag phase in methanogenesis due to disturbance (Souto et al., 2010)), and closed off with a septum. At Lake Kemnade, additional bottles were set up containing similar amounts of sediment and 30 g FW of *E. nuttallii*. This treatment was added to study the effect of dense vegetation on net CH_4 production by either promoting (anaerobic) CH_4 oxidation or methanogenesis. After setting up the incubations, bottles were flushed with N_2 gas (OFN, grade 2; 5 mins for Hartbeespoort Dam and 20 mins for Lake Kemnade) to ensure anoxic conditions (DO concentrations <1 mg L^{-1} were measured in bottles at Hartbeespoort Dam). At Lake Kemnade, samples were collected from the bottles after 0, 2 and 20 h, using the same method as described above for total methane fluxes. To maintain constant pressure in the bottle, the extracted sample volume was simultaneously replaced by inserting anoxic, filtered (0.7 µm) lake water (obtained by flushing with OFN for 15 mins) through the septum. At Hartbeespoort Dam, the bottles were too small for repeated sampling. Four parallel series of incubations were set up, to allow bottles to be sacrificed after 0, 3, 22 and 46 h by injection with $ZnCl_2$ (50%, 15 µL) to halt microbial activity after vigorous mixing. Methane concentrations were measured as described above, and potential methane production was determined from the increase in CH_4 over time and corrected for sediment dry weight. The following formula was used for this:

$$MG_i = \frac{\left(\frac{\Delta C_h * V_h + \Delta C_i * V_w * \alpha}{\Delta t}\right)}{M_s} \qquad [3.3]$$

where MG_i represents potential methanogenesis (in nmol g DW h) in vial i, C_h represents the methane concentration in the headspace, V_h the volume of the headspace, V_w the volume of the water layer, a the Bunsen coefficient, t is time in hours and M_s is the dry weight of the sediment.

3.2.6 Environmental variables

At all locations, water samples (n = 5 per time point) were collected one week before and one week after macrophyte removal at the impact and control sites. At Lake Kemnade and Lake Grand-Lieu, additional samples were collected immediately after and six weeks after plant removal. At Lake Kemnade and Hartbeespoort Dam, sampling was repeated 2-3 times in the same week (between 9 and 11 am). At the time of sampling, pH, conductivity, water temperature and dissolved oxygen (DO) concentrations were recorded at the same locations. Water samples were fixed in the field with 2 N HCl and brought to the laboratory for analyses (samples from France and SA were transported while frozen; Lake Kemnade samples were kept at 4°C during transport). Chlorophyll-a (Chl-a) content was determined by filtering a known amount over a GF/F (Whatman; 0.7 µm) filter, which was frozen at -80°C until analyses for content of chlorophyll-a using high-performance liquid chromatographic (HPLC, Shatwell et al., 2012). Additionally, temperature and DO concentrations (Minidot Logger, PME, U.S.A.) and relative light levels (HOBO Temperature/Light data logger, Onset, U.S.A.) were logged continuously at 20 cm below water surface and 20 cm above sediment surface at Lake Kemnade and Hartbeespoort Dam. Unfiltered water samples were analysed for total phosphorus (TP) and total organic carbon (TOC) concentrations. TP analyses were carried out photometrically after digestion with 10 N sulfuric acid and 30% hydrogen peroxide. TOC concentrations were determined using a TOC analyser (Shimadzu TOC-LCPN with an TNM-L (Total Nitrogen Measuring unit)). Filtered samples (using 0.45 µm filters) were analysed colourimetrically for nitrate (NO_3^-) and ammonium (NH_4^+) using a continuous flow analyser (SEAL Analytical AutoAnalyzer AA3 with AACE Software 7.10).

3.2.7 Vegetation

At each of the three lakes, the macrophyte biomass was quantified one week before and one week after macrophyte removal. Biomass was collected from within a set quadrat (0.16 m^2) at 5 randomly chosen locations in both the impact and the control site. Harvested plant material was weighed (after shaking to remove excess water) to determine fresh weight, then oven-dried at 60°C until stable weight. Using the quadrat size, biomass was then converted to g DW m^{-2}. At Lake Kemnade, vegetation cover and height were determined before, after and six weeks after removal. Using these data, the biomass (in g DW m^{-2}) could be estimated six weeks after removal of *E. nuttallii*.

3.2.8 Statistics

Differences in water chemistry parameters (pH, concentrations of NO_3, NH_4, TP, TOC, DO, Chl-a) and macrophyte biomass between lakes were determined by one-way ANOVAs, with Tukey HSD post-hoc tests for the control sites. For the TP concentrations at Lake Grand-Lieu, we ran a Rosner's Test to identify three outliers, which were removed from the dataset. Two-way ANOVAs were used to determine the impact of macrophyte removal on the same physical and chemical parameters within each lake. Linear mixed models were used to test whether macrophyte removal impacted diffusive CO_2 and CH_4 emission and total CH_4 emission in the three lakes. Before applying models, data were checked for normality and homogeneity by visual inspection of boxplots and histograms and log-transformed when needed. Rosner outlier analyses were run on visual apparent outliers, using the EnvStat package (Millard and Kowarik, 2020), and removed when found to be significant outliers. Models were built with Site (control or impact) and Time (before or after removal) as fixed effects. Replicate ID for each lake was included as a random effect to account for repeated sampling. To determine the effect of removal, models including the interactive term between Site and Time were compared with models where this interaction was dropped using the log likelihood ratio (LLR). Estimated marginal means were used for pairwise comparison between time points when the interaction between Site and Time was significant and multiple time points were included. 'Time of Day' was added as an additional fixed factor but only improved model fit when determining effect on CO_2 fluxes. It was therefore removed from models describing diffusive and total CH_4 fluxes.

To determine whether potential CH_4 production rates of the sediment differed between Lake Kemnade and Hartbeespoort Dam, a Student's t-test was used. Similarly, the difference in potential CH_4 production between the sediment-only treatment from Lake Kemnade and the treatment containing both sediment and *E. nuttallii* was tested with a Student's t-test. Differences between depth profiles of dissolved CH_4 concentrations in the rhizosphere at control and impact sites in Hartbeespoort Dam were determined using a Linear Mixed Model, with Depth (cm), Time (before and after removal) and Site (Impact and Control) as fixed factors and Replicate ID as random factor to account for repeated sampling (in depth profile, rather than time).

Boosted regression tree (BRT) models (De'ath and Fabricius, 2016) were used to identify environmental variables that best describe patterns in diffusive CO_2 and CH_4 flux in Hartbeespoort Dam and Lake Kemnade. The set of predictor variables consisted of macrophyte biomass (g DW m^{-2}), total phosphorus (TP; µmol L^{-1}), dissolved oxygen saturation (DO; %), water temperature (°C), pH, total organic carbon (TOC; µmol L^{-1}), and chlorophyll-a (µg L^{-1}). Moreover, time of day was also used as a predictive variable to account for photosynthetic activity. The variables time (before, during and after removal) and site (control and impact) were likewise included in the BRTs. In the BRTs for diffusive CO_2, DO and pH were initially included, but since these are collinear and a product of macrophyte photosynthesis, DO and pH were excluded in the final models. A detailed description of the BRT models and results (including figures) can be found in the Supplementary Information.

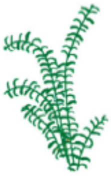
All statistical analyses and graphics were performed in R version 6.3.3 (R Core Team, 2020) using the following packages: lme4 (Bates et al., 2021, p. 4), gbm (Greenwell et al., 2020), dismo (Hijmans et al., 2021) emmeans (Lenth et al., 2022), EnvStats (Millard and Kowarik, 2020) and ggplot2 (Wickham et al., 2020).

3.3 RESULTS

3.3.1 Effect of macrophyte removal on lake characteristics

The control and impact sites had comparable amounts of biomass per m^2 before macrophyte removal (Table 1) in each of the three lakes. Mowing removed 100%, 73% and 100% of macrophyte biomass in Hartbeespoort Dam, Lake Kemnade and Lake Grand-Lieu, respectively. All remaining *E. nuttallii* biomass in the impact site at Lake Kemnade was present in the bottom 50 cm due to limitations of the mowing boat. Chemical composition of the lake water differed between the three lakes, but no effect of macrophyte removal was found. Similarly, most physical parameters did not change when macrophytes were removed, except for light availability, temperature and Chl-a concentrations. Removal of *E. nuttallii* increased light attenuation from <1-10% reaching 1.5 m depth (data not shown). At Hartbeespoort Dam, only about 1.3% of global radiation penetrated the *P. crassipes* canopy (data not shown). After removal, however, light attenuation increased from 1.7 m^{-1} to 2.1 m^{-1} due to phytoplankton growth. Chlorophyll-a concentrations in the water layer were approximately 14 times higher in the impact compared to the control site after *P. crassipes* was removed (Table 3.1). At Lake Grand-Lieu, Chl-a increased at both sites six weeks after removal (Table 3.1), while water temperature increased from 21.3 ± 1.7°C to 27.0 ± 1.7°C in the impact site only after removal (data not shown).

Table 3.1: Lake water characteristics and dominant macrophyte biomass at the three case study sites, presented as means ± standard deviation.

Lake	Site	Time	Biomass (gDW m^{-2})	pH	NO_3^- (μmol L^{-1})	NH_4^+ (μmol L^{-1})	TP (μmol L^{-1})	TOC (μmol L^{-1})	DO (% sat)	Chl-a (μg L^{-1})
Hartbeespoort Dam 	Impact	Before	972 ± 137	6.9 ± 0.4	18.8 ± 2.3	72.6 ± 1.9	27.1 ± 11.1	1218 ± 1049	5.9 ± 6.5	NA
		After	0	6.9 ± 0.2	20.6 ± 12.3	41.4 ± 41.1	27.6 ± 8.6	3222 ± 7685	70.9 ± 53.9	4108 ± 8981
	Control	Before	937 ± 383	7.6 ± 0.7	20.5 ± 1.0	74.2 ± 2.3	18.7 ± 13.2	845 ± 520	4.8 ± 4.6	NA
		After	1279 ± 320	7.7 ± 1.1	18.5 ± 9.3	15.8 ± 14.6	28.7 ± 9.1	987 ± 797	66.2 ± 48.8	295 ± 465
Lake Grand Lieu 	Impact	Before	183 ± 85	NA	1.2 ± 0.7	7.6 ± 2.3	21.6 ± 3.3	2320 ± 288	NA	177.4 ± 82.1
		After	0	8.0 ± 0.5	0.1 ± 0.0	3.6 ± 0.8	17.4 ± 7.1	1935 ± 111	36.2 ± 10.6	147.6 ± 18.0
		After 6	NA	8.9 ± 0.9	8.4 ± 14.1	12.9 ± 4.5	32.2 ± 1.2	3280 ± 198	115.7 ± 34.3	229.4 ± 118.9
	Control	Before	249 ± 54	NA	1.9 ± 1.6	14.3 ± 9.2	28.5 ± 8.8	2573 ± 841	NA	111.6 ± 10.1
		After	275 ± 101	7.4 ± 0.3	0.2 ± 0.3	4.0 ± 1.2	14.5 ± 2.7	1820 ± 80	59.6 ± 13.9	93.6 ± 24.3
		After 6	NA	7.4 ± 0.3	2.3 ± 0.9	10.0 ± 2.4	35.6 ± 5.5	2618 ± 412	35.8 ± 46.4	320.6 ± 43.7
Lake Kemnade 	Impact	Before	421 ± 180	10.0 ± 0.1	35.3 ± 9.0	2.5 ± 0.3	1.7 ± 0.6	483 ± 79	200 ± 3.2	30.0 ± 20.1
		After	112 ± 135	9.4 ± 0.3	24.2 ± 2.4	2.8 ± 1.1	1.8 ± 1.0	316 ± 40	152 ± 33.2	12.5 ± 4.0
		After 6	242 ± 71	NA	80.8 ± 2.3	2.0 ± 0.3	1.1 ± 0.4	285 ± 18	NA	4.0 ± 1.7
	Control	Before	591 ± 165	9.7 ± 0.9	35.7 ± 14.4	3.0 ± 0.6	2.0 ± 2.3	441 ± 75	154.9 ± 48.8	20.5 ± 18.3
		After	972 ± 276	9.0 ± 0.9	21.9 ± 7.4	1.4 ± 0.3	2.2 ± 1.3	404 ± 121	139.6 ± 53.2	31.5 ± 11.6
		After 6	479 ± 43	NA	81.4 ± 1.4	3.9 ± 0.4	1.8 ± 0.8	307 ± 19	NA	9.8 ± 10.5

3.3.2 Effect of removal on diffusive fluxes of methane and carbon dioxide

Removal of *E. nuttallii* and *P. crassipes* did not affect diffusive CH_4 emission in Lake Kemnade and Hartbeespoort Dam (Figure 3.2), which ranged from 0.2 to >10 mg C m-2 h-1 (median 1.07) and from 0.1 to >15 mg C m^{-2} h^{-1} (median 1.24), respectively. The BRTs showed that diffusive CH_4 emissions from both lakes were best explained by water temperature (both 29%) and DO concentrations (23-30%) (Supplementary Information 1). At Lake Kemnade, both impact and control site showed net CO_2 fixation during daytime, with fluxes of approximately -10 to -80 mg C m^{-2} h^{-1} (Figure 3.3). Fixation was higher in the control (median -59 mg C m^{-2} h^{-1}) than in the impact (median -38 mg C m^{-2} h^{-1}) site. Time of day had a strong influence on CO_2 fluxes ($p = 0.008$, LLR = 7.0, df = 1), with fluxes becoming more negative from morning to late afternoon in both control and impact site (indicating increased C-fixation). Immediately after removal of *E. nuttallii*, CO_2 fluxes increased rather than decreased during the day. This 3-way interaction was only a trend ($p = 0.075$, LLR = 6.9, df = 3), and 1 week after removal, no differences were observed in daily CO_2 patterns between impact and control site. This effect of removal contrasts with observations at Hartbeespoort Dam (Figure 3.3). Here, daytime CO_2 fluxes were very high before removal (100-300 mg C m^{-2} h^{-1}). After removal of *P. crassipes*, the impact site showed negative daytime fluxes (median -9.4 mg C m^{-2} h^{-1}), indicating photosynthetic activity of phytoplankton, while the control site remained a net CO_2 source (105 mg C m^{-2} h^{-1}; $p < 0.001$, LRR = 18.9, df = 1). The BRTs also showed contrasting results for the two lakes. At Lake Kemnade, CO_2 fluxes were best explained by water temperature (23%), time-of-day (14%) and macrophyte biomass (13.5%), whereas in Hartbeespoort Dam water temperature (33%), TOC (30%) and Chl-a. (22%) explained most variation in CO_2 fluxes.

3.3.3 Effect of removal on total fluxes of methane

Removal of *Ludwigia* from Lake Grand-Lieu showed no clear effect on total CH_4 emission (Figure 3.4). Compared to the Lake Kemnade and Hartbeespoort Dam, total emission of CH_4 was high, with rates between 3.5 and 48 mg C m^{-2} h^{-1}. Although fluxes were lower in the impact site compared to the control site, this difference already existed before removal and could not be attributed to presence or absence of *Ludwigia*. After removal, the total CH_4 flux seemed to decrease in the control site while remaining the same in the impact site, whereas at six weeks after removal, fluxes had increased in both impact and control site.

At Lake Kemnade, total CH_4 emission in the impact site was reduced following the removal of submerged *E. nuttallii* ($p = 0.01$, LLRinteraction = 10.9, df = 3; Figure 3.4). Fluxes dropped from 2.6 to 1.1 mg C m^{-2} h^{-1} (a decrease of 58%) immediately following removal and were lower than in the control site both immediately ($p = 0.009$; estimated marginal means) and one week ($p = 0.09$; estimated marginal means) after removal. While total emission in the impact site returned to approximately 2.6 mg C m^{-2} h^{-1} one week after removal, the control site meanwhile showed an increase from 8.3 to 10.4-12.2 mg C m^{-2} h^{-1} (an increase of 24-47%). This increase at the control site was likely correlated with an increase in average water temperature from 22° to 26°C in this period. Six weeks after removal, in early autumn, rates had dropped again to approximately 1.4 and 2.0 mg C m^{-2} h^{-1} at the impact and control site, respectively. At the control site, the contribution of ebullition to the total flux was 62-85% (Table 3.2). At the impact site, ebullition accounted for 84% before removal, but immediately and one week after, this contribution was brought down to 0%. After six weeks, ebullition again constituted about 80% of the total flux at the impact site. The lowest total CH_4 fluxes were recorded at Hartbeespoort Dam (Figure 3.4). Here, fluxes in *P. crassipes* mats ranged from 0.01 to 2.20 (median 0.8) mg C m^{-2} h^{-1}. Macrophyte removal increased the total flux to approximately 0.6-9.0 (median 2.2) mg C m^{-2} h^{-1} ($p = 0.023$, LLR = 5.2, df = 1), while fluxes in the control site remained unchanged. This increase in total flux was mainly due to ebullition, which did not add to the CH_4 emission before removal but accounted for about 60% of the flux one week after *P. crassipes* was removed (Table 3.2). Simultaneously, removal of *P. crassipes* reduced the concentration of dissolved CH_4 along a depth gradient in the top 20 cm of the water layer ($p = 0.006$, F= 8.1, df=1). With an intact floating mat, dissolved CH_4 ranged from 159 ± 112 nmol L^{-1} in the top 5 cm to 106 ± 137 nmol L^{-1} around 20 cm depth, whereas after *P. crassipes* removal, concentrations ranged from 28 ± 26-65 ± 32 nmol L^{-1} at 5 and 20 cm depth, respectively.

3.3.4 Potential methane production

Potential CH_4 production rates in sediments were higher at Hartbeespoort Dam (4.5 ± 2.0 nmol g DW^{-1} h^{-1}) than at Lake Kemnade (1.1 ± 0.5 nmol g DW^{-1} h^{-1}; $p = 0.008$, F = 7.84, df = 2). (Figure 3.5). At Lake Kemnade, presence of *E. nuttallii* doubled the potential CH_4 production ($p = 0.015$, F = 9.55, df = 1). Using the potential CH_4 production (per ℓ sediment used in the incubations) and assuming an active sediment layer of 20 cm (Wilkinson et al., 2015), Lake Kemnade and Hartbeespoort Dam would see a sediment CH_4 production rate of approximately 0.64 ± 0.27 and 0.26 ± 0.31 mg CH_4^- C m^{-2} h^{-1}, respectively.

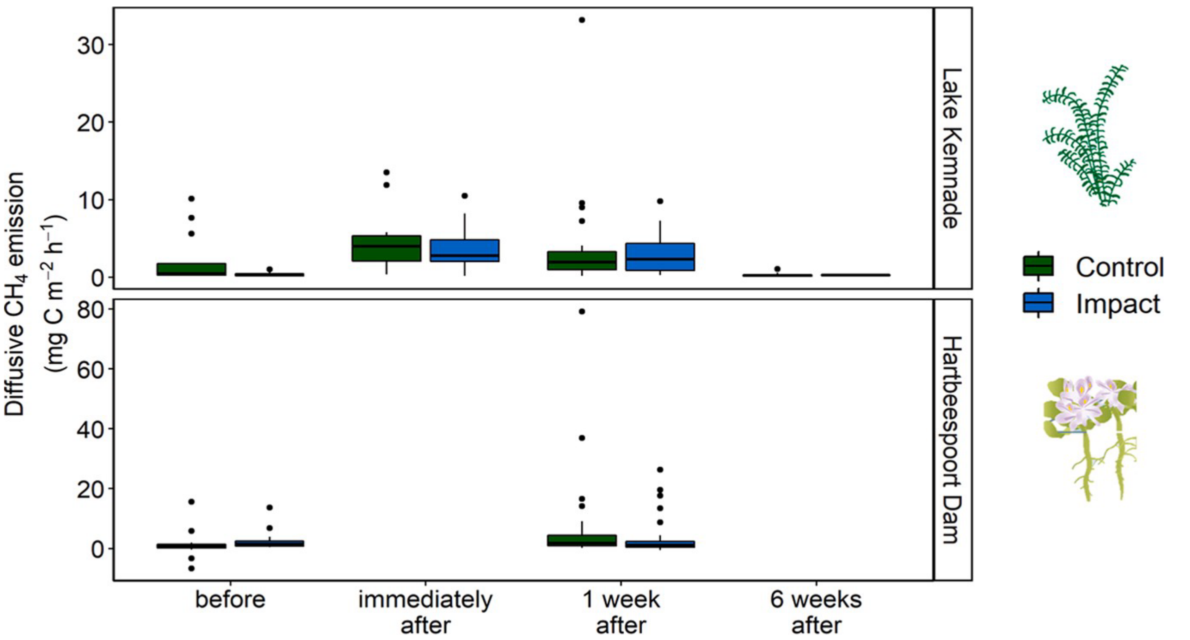


Figure 3.2: Diffusive flux of methane from Lake Kemnade (top; n.s.) and Hartbeespoort Dam (bottom; n.s.), before and after removal of macrophytes *(Elodea nuttallii* and *Pontederia crassipes*, respectively). At Lake Kemnade, fluxes were also measured immediately after removal and six weeks after. Mind the different scales on the y-axis. Horizontal bold lines indicate the median, boxes the 25% and 75% percentiles, and whiskers the minimum and maximum values. Points represent outliers.

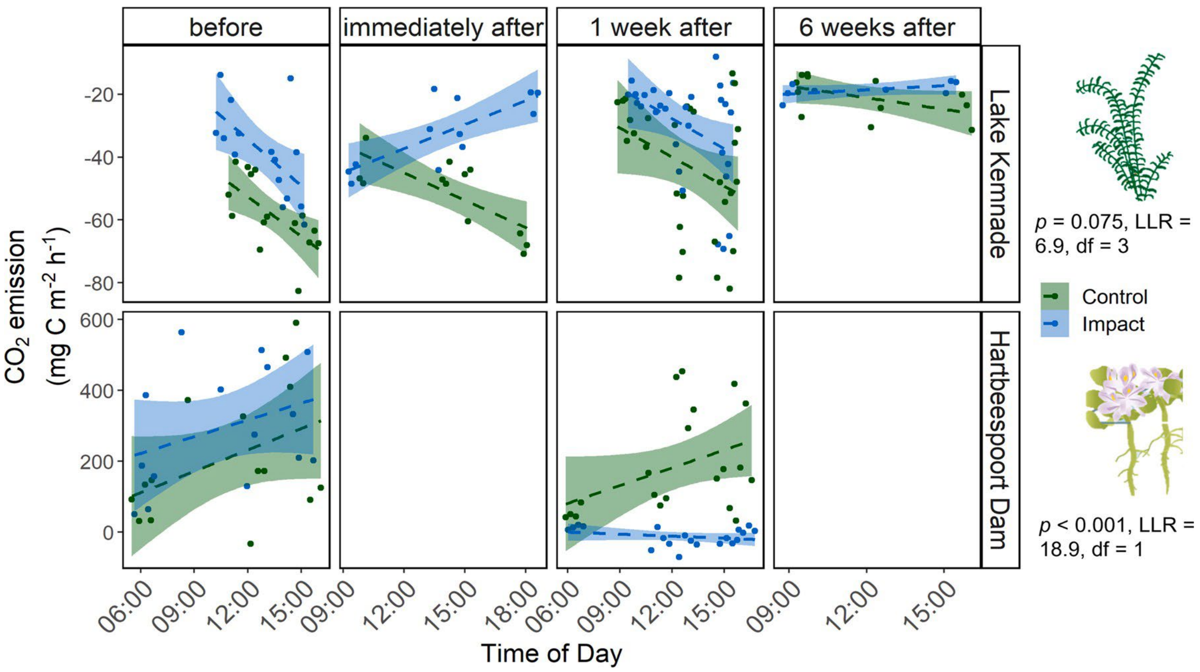


Figure 3.3: Diffusive fluxes of CO_2 against time of day, measured in the impact and control sites at Lake Kemnade, before, immediately after, one week after and six weeks after removal of *Elodea nuttallii*, and at Hartbeespoort Dam before and one week after removal of *Pontederia crassipes*. Mind the different scales on the y-axis. Statistical information is given on the interactive effect of Site, Time and Time-of-Day.

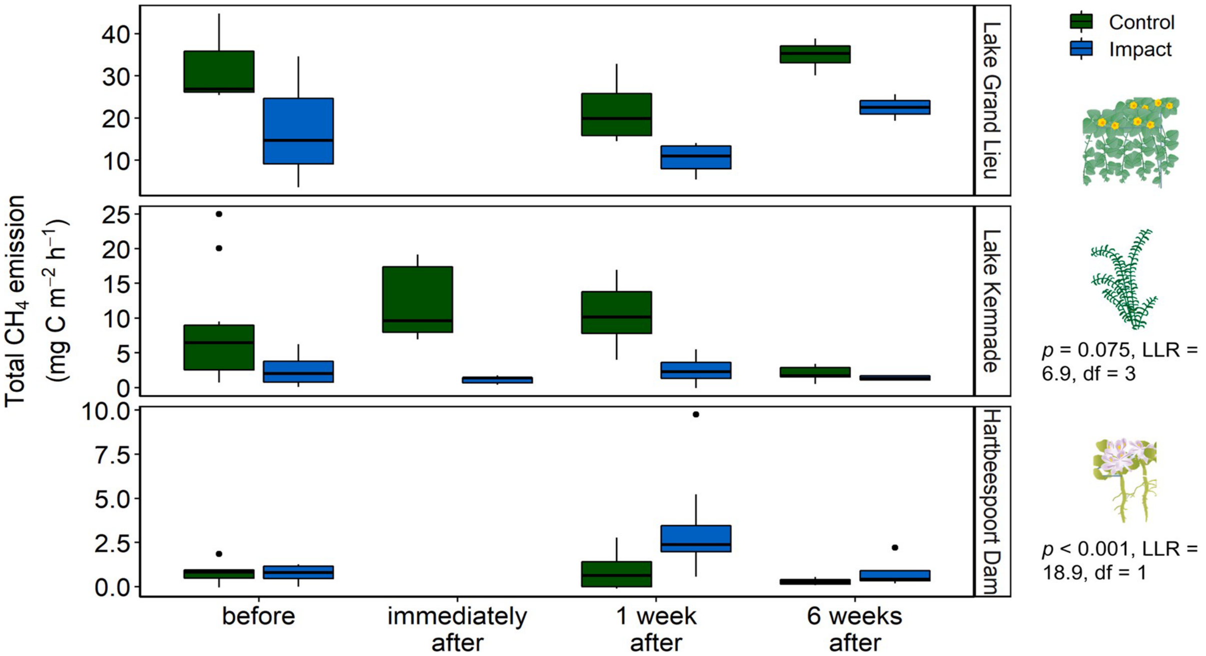
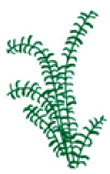


Figure 3.4. Total flux of CH_4 determined in Lake Grand-Lieu (top), Lake Kemnade (middle) and Hartbeespoort Dam (bottom) before, immediately after and one after and six weeks after removal of invasive macrophytes (*Ludwigia* spp., *Elodea nuttallii*, *Pontederia crassipes*, respectively). Note different scale of the y-axis for the three lakes. Horizontal bold lines indicate the median, boxes the 25% and 75% percentiles, and whiskers the minimum and maximum values. Points represent outliers. Statistical information is given on the interactive effect of Site and Time.

Table 3.2: Rates of total, diffusive and ebullitive CH_4 fluxes for Hartbeespoort Dam, Lake Kemnade and Lake Grand-Lieu. Average measured diffusive CH_4 fluxes (including plant-mediated CH_4-transport) were subtracted from the measured total fluxes to determine rates and relative contribution of ebullition. Fluxes are displayed as mean ± sd. Significant outliers (Rosner's Test) were excluded in this estimation of the contribution of ebullition.

Lake	Site	Time removal	Total (mg C m^{-2} h^{-1})	Diffusive (mg C m^{-2} h^{-1})	Ebullition (mg C m^{-2} h^{-1})	Ebullition (%)
Hartbeespoort Dam	Impact	Before	0.8 ± 0.5	1.9 ± 1.7	~0	~0
		After 1 week	3.4 ± 2.9	1.3 ± 1.9	2.1	61
	Control	Before	0.8 ± 0.5	1.5 ± 4.6	~0	~0
		After 1 week	0.9 ± 1.1	2.1 ± 2.1	~0	~0
Lake Kemnade	Impact	Before	2.6 ± 2.2	0.4 ± 0.3	2.2	84
						

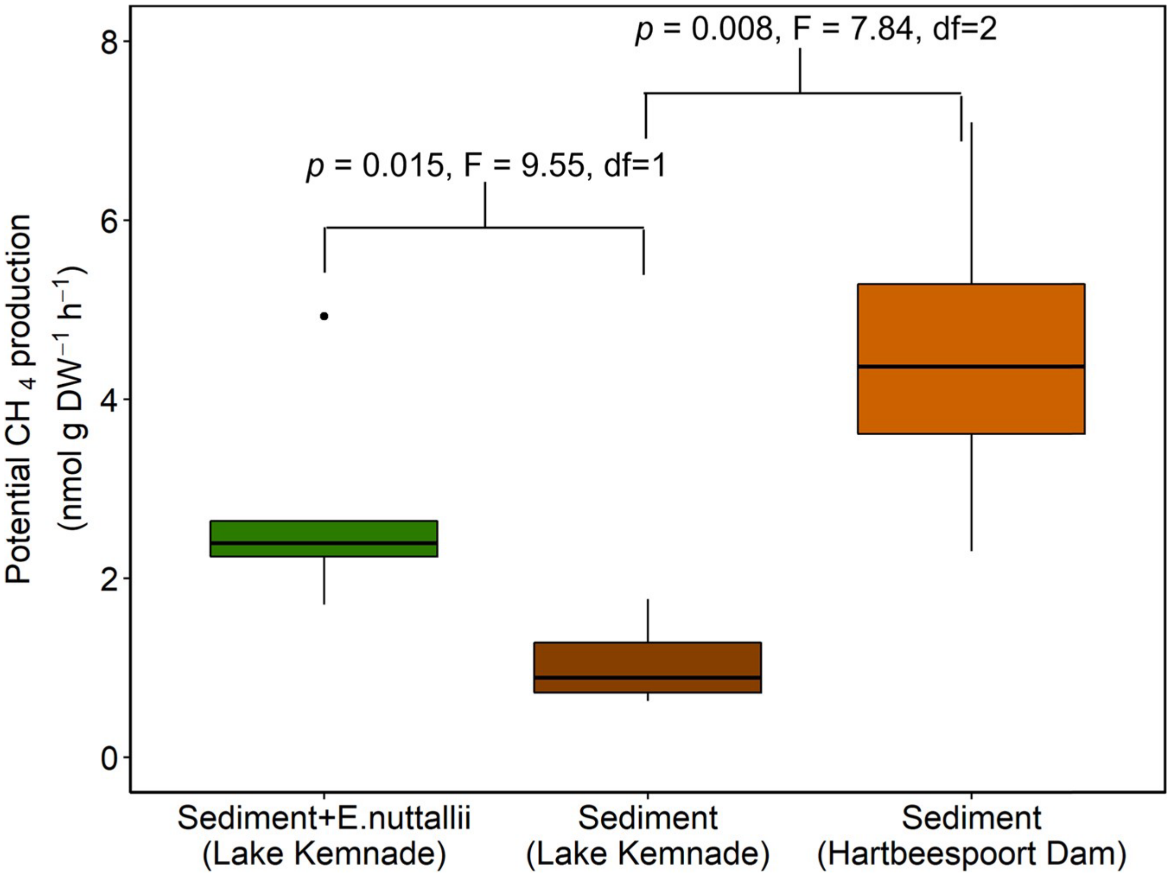


Figure 3.5: Potential hourly methane production, derived from incubations of sediment with (left) or without (middle) *E. nuttallii* at Lake Kemnade, and sediment at Hartbeespoort Dam (right).

3.4 DISCUSSION

3.4.1 Short-term effect of macrophyte removal on CO_2 emission

Macrophyte removal had a different impact on CO_2 emission in Lake Kemnade and Hartbeespoort Dam, which are dominated by submerged *E. nuttallii* and free-floating *P. crassipes*, respectively (Figure 3.6). Despite our use of opaque chambers, significant daytime CO_2 uptake rates were measured at Lake Kemnade, which were reduced after removal of *E. nuttallii*. This was especially apparent at times when peak photosynthetic activity occurs, between noon and late afternoon, and the difference was strongest immediately following removal. As the mowing boat could not remove the bottom 50 cm of *E. nuttallii*, the remaining plants, possibly together with a modest growth of phytoplankton ensured that CO_2 was still being fixed during the day at reduced rates. Immediately after removal, photosynthetic activity was most likely limited by turbidity caused by disturbance of the sediment. One week after removal, daytime CO_2 fixation patterns had recovered to rates recorded before removal as sediment disturbance decreased and remaining *E. nuttallii* started to regrow. Average fixation rates one week after removal were about 25% lower than before removal, which is still remarkable given that only 27% of the vegetation biomass remained. *E. nuttallii* is known to be highly adapted to disturbance by both herbivory and removal and has a high relative growth rate (He et al., 2019). Six weeks after removal, *E. nuttallii* had already doubled its biomass compared to one week after removal, thus reaching an average growth rate of 3.7 g DW m-2 d-1.

At Hartbeespoort Dam, *P. crassipes* stands showed very high daytime CO_2 emission rates of 100-300 mg C m^{-2} h^{-1} before removal. Our findings contrast with previous studies that have found that *P. crassipes* can often offset CO_2 emissions in freshwater systems (Oliveira Junior et al., 2021; Peixoto et al., 2016), due to its high primary production under nutrient-rich conditions (Junk and Howard-Williams, 1984). A previous study in the Amazon and Pantanal has reported very high daytime CO_2 uptake rates of -1000 ± 500 mg C m^{-2} h^{-1}, which compensated for night-time emissions, resulting in a net CO_2 sink (Oliveira Junior et al., 2021). The contrasting findings in our study could result from using opaque chambers, as we exclude the direct uptake of CO_2 from the atmosphere by *P. crassipes*. However, as we observed a strong decrease in *P. crassipes* cover at Hartbeespoort Dam during the summer of 2019 and 2020, damage to the plants by the biological control agent *Megamelus scutellaris* most likely also played a role in the high CO_2 fluxes measured at this lake. After removal, the system showed net CO_2 uptake, due to the explosive growth of phytoplankton in the absence of light limitation. In addition, this cyanobacterial bloom may have benefitted from the removal of *P. crassipes*, since the species is known to produce allelopathic substances that inhibit cyanobacterial and algal growth (Pei et al., 2018).

Rates are based on measurements conducted at the impact sites before and one week after macrophyte removal and are expressed in mg C m^{-2} h^{-1}. Width and direction of the arrows indicate proportion and direction of the CO_2 and CH_4 fluxes. The impact of macrophytes on diffusive CO_2 fluxes at Lake Kemnade and Hartbeespoort Dam were confirmed by the boosted regression trees, which showed that macrophyte presence explained 15.4% and <5% respectively. This is low compared to other factors that influence CO_2 emission, such as temperature (22-33%), Chl-a. (13-21%) and TOC (30%). These findings thus suggest a small direct effect of macrophytes on CO_2 fluxes. The environmental factors, such as temperature and Chl-a content could, however, be affected by macrophyte presence themselves. Macrophyte removal raised water temperature at Lake Grand-Lieu and Chl-a concentrations at Hartbeespoort Dam. Macrophyte presence could thus have direct and indirect effects on greenhouse gas emission.

3.4.2 Short-term effect of macrophyte removal on CH_4 emission

Although macrophyte dominated lakes are often sinks for CO_2 (Kosten et al., 2012), these systems can be important sources of CH_4 emission (Aben et al., 2017). Anoxic sediments, especially those with higher organic matter contents, provide ideal conditions for methanogens. The sediments of both Lake Kemnade and Hartbeespoort Dam showed potential CH_4 production rates, which roughly correspond with emissions of 0.3-0.6 mg CH_4 -C m^{-2} h^{-1}. This is slightly lower than the total fluxes of CH_4 that we determined at these lakes (but still in the same order of magnitude), which may have resulted from a lag phase in the incubation due to disturbance during set-up (Souto et al., 2010). Potential rates of methanogenesis in the incubations doubled when *E. nuttallii* was present. This indicates that the growth of dense macrophyte stands can substantially affect CH_4 dynamics in freshwater lakes, for example by providing easily degradable organic matter or through plant-mediated methane transport (see review by Joabsson et al., 1999). Lake Grand-Lieu, which experiences mass development by invasive, emergent *Ludwigia* species, showed a high total CH_4 emission that appeared unrelated to macrophyte presence. Therefore, it is implied that either plant-mediated CH_4 emission did not contribute significantly to the total flux during the investigated period, or that CH_4 oxidation in the rhizosphere counterbalanced the plant-mediated CH_4 transport. Another possibility is that plant-mediated CH_4 transport has been limited due to the use of opaque chambers lowering convective flow (Chanton et al., 1993), thereby underestimating CH_4 fluxes in *Ludwigia* dominated plots. Due to travel restrictions, we were unfortunately unable to determine diffusive fluxes in this system and can therefore not give an estimate of the relative contribution of the pathways of ebullition and diffusion. Lake Grand-Lieu is a very shallow system and our study sites had a water layer of 30-50 cm, low oxygen saturation and high TOC and TP concentrations. This high availability of organic carbon and TP could have resulted in a high biological oxygen demand, thus lowering the oxygen concentration in the water layer. Decaying mats of *Ludwigia* species have been known to cause anoxic conditions in shallow systems, with negative impact on fish and other fauna (Nehring and Kolthoff, 2011). Although *Ludwigia* was removed completely from our impact site, the high availability of TOC and TP remained and was possibly enhanced by sediment disturbance or phytoplankton growth. Both anoxic conditions and the availability of substrates for microbial metabolism could have stimulated the production of CH_4 at this lake, while the low oxygen concentrations would have limited CH_4 oxidation, resulting in high emission rates.

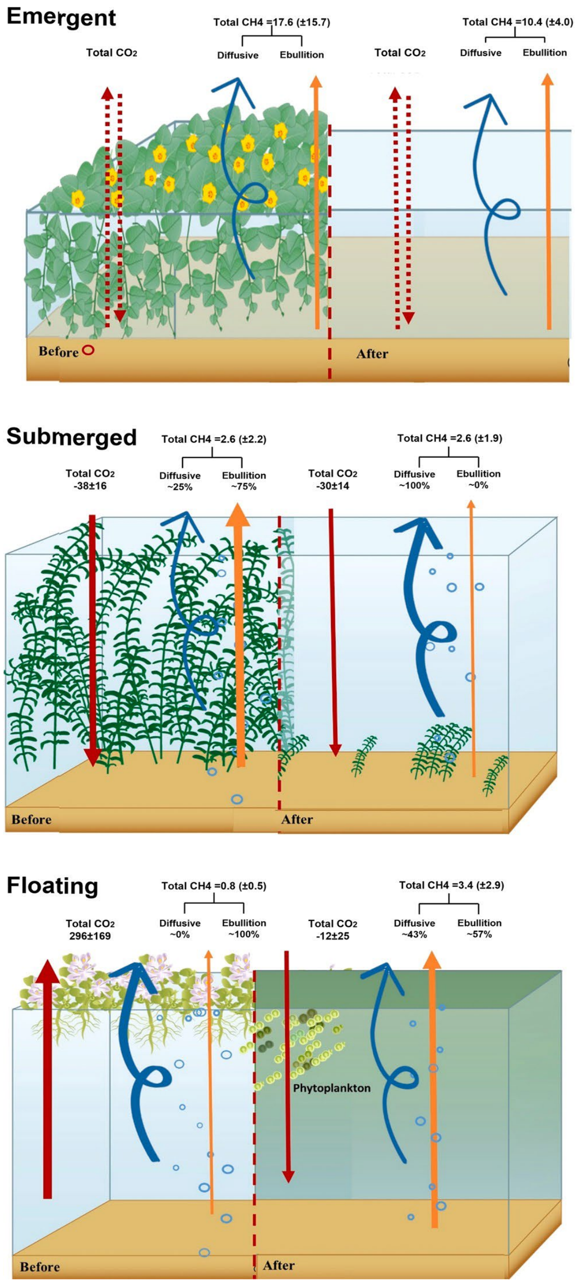


Figure 3.6: Lake Grand-Lieu, Lake Kemnade and Hartbeespoort Dam (top to bottom) showed contrasting short-term responses in CO_2 and CH_4 fluxes after removal of their respectively mass developments of macrophytes. At Lake Grand-Lieu, the high total CH_4 fluxes did not seem to be impacted by the removal of macrophytes. Rather, a combination of high TOC availability, low DO and high temperatures most likely stimulated methanogenesis and limited methane oxidation in this shallow system. At Lake Kemnade, removal of the top layers of the *E. nuttallii* vegetation temporarily decreased CO_2 fixation (red arrows) but also CH_4 emission (blue and orange arrows). This was most likely caused by outgassing of CH_4 due to disturbance of the sediment by the mowing boat. At Hartbeespoort Dam, removal of the floating *P. crassipes* stimulated growth of phytoplankton, which resulted in net CO_2 uptake (red arrows). Simultaneously, the total CH_4 emission (blue and orange arrows) strongly increased after removal of the barrier of floating vegetation, which normally captures CH_4 and could stimulate CH_4 oxidation in the rhizosphere.

Removal of submerged *E. nuttallii* appeared to reduce CH_4 ebullition at Lake Kemnade but not diffusive CH_4 fluxes (Figure 3.6). While ebullition contributed approximately 63-85% to the overall CH_4 flux in vegetated control sites, it became negligible after removal of *E. nuttallii*. The most likely explanation for this is outgassing due to sediment disturbance during mowing. Although the mowing boat left approximately 50 cm of *E. nuttallii* growing on (and rooting in) the sediment, the physical removal and possibly shear stress caused by the large boat, will most likely have disturbed the upper sediment layers where bubbles had built up over time (Maeck et al., 2014). Simultaneously, while the control site showed an increase in total CH_4 emission over time, fluxes at the impact site remained low. This could indicate that methane production at the impact site had not yet returned to the pre-disturbance levels of bubble production. In a controlled laboratory study, Liu et al. (2016) observed a lag phase of approximately six days during which ebullition was negligible, with normal bubble production resuming after approximately 12 days (Liu et al., 2016). Our incubation experiment suggests a more direct effect of *E. nuttallii* on CH_4 fluxes, possibly by providing organic substrates for methanogenesis. Higher CH_4 fluxes from submerged vegetation than from non-vegetated zones have also been found in lakes (Zhang et al., 2019) and reservoirs (Cronin et al., 2006), and could be due to decaying biomass at the sediment surface providing organic substrate for methane production (Joabsson et al., 1999). This does not explain, however, why the difference in CH_4 emissions was only observed in total fluxes and not in diffusive fluxes.

At Hartbeespoort Dam, the diffusive fluxes of CH_4 were highly variable in both impact and control site and did not show an effect of macrophyte removal. Total CH_4 fluxes, however, showed a threefold increase when *P. crassipes* was removed. As *P. crassipes* did not root in the sediment at our study sites (Oliveira Junior et al., 2021), we assume plant-mediated methane transport did not play a substantial role and that the total flux is made up of diffusive fluxes and ebullition (Figure 3.6). While the contribution of ebullition was negligible in *P. crassipes* mats, the total flux comprised of 60% ebullition-derived methane and 40% diffusive methane after removal. In dense floating mats, the gaseous exchange across the water-atmosphere interface can be strongly reduced and floating leaves can 'capture' the gas bubbles (Kosten et al., 2016), which then accumulate in the rhizosphere. Here, methanotrophs (A´vila et al., 2019) could oxidise this methane, thus further lowering emission to the atmosphere (Yoshida et al., 2014). This capturing of CH_4 is also illustrated by the higher dissolved CH_4 concentrations found in the rhizosphere of *P. crassipes* mats compared to the top 20 cm of the water layer after *P. crassipes* removal. By bringing the ebullition-pathway almost to zero, the mat of *P. crassipes* effectively reduced the emission of methane by an estimated 0.8-1.1 mg C m^{-2} h^{-1}, supporting the results of several studies reviewed by Kosten et al. (2016).

As with the diffusive CO_2 fluxes, the boosted regression trees indicated that the magnitude of direct effect of macrophytes on CH_4 fluxes was small, since macrophyte presence (in biomass) explained less than 5% of the variation in CH_4 fluxes. Environmental variables such as temperature (28-29%), dissolved oxygen (23-30%) and pH (24%) were the main factors explaining the patterns in CH_4 fluxes, as has also been reported in previous studies (e.g. Oliveira Junior et al., 2021). Again, the results of the BRTs may obscure the indirect effects that macrophytes have on the environmental factors that form the main explanatory variables.

3.4.3 Implication for management of shallow lakes with mass developments of macrophytes

Our three lakes each display their own unique combination of invasive macrophyte, environmental conditions and climate, and in each lake, macrophytes are removed for different reasons. As hypothesised, macrophyte removal had contrasting short-term effects on the CH_4 and CO_2 emission from these lakes. Additionally, it was expected that the overall C emission would increase following removal. At Lake Grand-Lieu, we could not determine the full effect of removal on C-emission as the CO_2 fluxes could not be measured. It can be assumed, however, that the removal of invasive *Ludwigia* would lower CO_2 fixation. As there was no effect of removal on the CH_4 emission at this lake, it is believed that overall would increase C emission at Grand-Lieu. At Hartbeespoort Dam, removal resulted in a strong increase in CH_4 emission, which fits with the hypothesis that the removal of floating vegetation has a greater impact on CH_4 fluxes than removal of sub-merged and emergent macrophytes. Although a cyanobacterial bloom caused nett CO_2 fixation after removal, this would most likely not outweigh the C-uptake by a healthy stand of *P. crassipes* (~1000 mg C m^{-2} h^{-1}; Oliveira Junior et al., 2021). Application of biological control agents, as is the current management practice at Hartbeespoort Dam, could, however, have strongly reduced the nett C-uptake by damaging the vegetation. While this biological control thus seems effective, it would be recommended that management at the lake focuses on reducing the nutrient input, since removal of *P. crassipes* most likely will result in recurring cyanobacterial blooms.

At Lake Kemnade, our measurements of CO_2 and CH_4 fluxes allow us to make a rough estimate of the effect of removal on the overall C emission. At the lake, approximately 47 of the 125 ha are covered by *E. nuttallii* (Ruhrverband, 2020). Without mowing, this area would see daytime CO_2 fixation of 340 kg C and a CH_4 emission of 70 kg C per day (using our average flux measurements from Table 2). This corresponds to a global warming potential (GWP) of 1367 kg CO_2 equivalents (using a GWP100 of 28 CO_2-eq. for CH_4) With a maximum capacity of 15.5 tons *E. nuttallii* removed per day by the mowing boat, approximately 9 ha can be mowed per week. Assuming that at any given time in the growing season, 9 ha is being mowed, 9 ha has just been mowed (1 week after) and 29 ha has regrown or remains vegetated, this lake would see day-time CO_2 fixation of 290 kg C and a CH_4 emission of 50 kg C per day, thereby reducing the GWP by ~40% to 803 kg CO_2-eq. Although contradicting the hypothesis that C emission would increase after macrophyte removal, this rough calculation omits the probable outgassing of CH_4 due to disturbance of the sediment. These events may be included in future research, for example by using Eddy Covariance. In addition, for a full C-budget, night-time CO_2 measurements should be included, as well as the C emission of decomposing biomass after removal.

Macrophyte management in systems experiencing mass developments is carried out to relieve nuisance growth, usually for recreational activities. The consequences of macrophyte removal on ecosystem functioning, however, are rarely quantified. If macrophyte management is reviewed, it is often limited to determining effects on water quality and the occurrence of phytoplankton blooms. Given the current emphasis on reducing greenhouse gas emissions to reach the targets set by the Paris agreement, it is important to understand how management of freshwater systems impacts their contribution to the global green-house gas budget. Apart from the short-term effects here presented, there is a strong need to determine the long-term impact of macrophyte removal on whole lake carbon budgets to develop sustainable management strategies.

CHAPTER 4: DEVELOPMENT OF CONCEPTUAL BAYESIAN NETWORKS (BNS) FOR MASS DEVELOPMENT OF AQUATIC PLANTS AND ITS MANAGEMENT[3]

4.1 INTRODUCTION

Quantification of multiple pressures and impacts requires integrative modelling (e.g. Grace et al., 2016) to optimise management solutions. The aim of WP2 was to draft models based on existing knowledge from the literature and project partners including key stakeholders. WP2 uses Bayesian Network models (BN). BNs enable the use of different types of information to be linked by conditional probability tables, so that when the probability distribution of a node in the network changes, its effect can be propagated through the network (e.g. Moe et al., 2021).

4.1.1 Causes of mass development: biophysical model

The likelihood of mass development of aquatic plants increases with resource availability and decreases with magnitude of disturbance events. Resources may be constrained by the growth form (submerged versus floating, access to atmospheric CO_2 – Sand-Jensen and Frost-Christensen, 1998), light (photosynthetic active radiations – Binzer et al., 2006), and dissolved CO_2 availability (Blackmann and Smith, 1911, could also include HCO_3 availability (Maberly and Madsen 2002)) – all together characterising the growth potential. The growth potential may be impaired by the availability of nutrients such as N and stoichiometric ratios such as N:P (Moe et al., 2019). Aquatic plant mass development also depends on factors removing or destroying plant tissue such as grazing (Bakker et al., 2016), freezing and water turbulence (Rørslett and Johansen, 1996). Grazing also depends on nutrient availability (Grutters et al., 2016), temperature and presence of specific grazers (used in biotic control, Hill and Coetzee, 2017). This forms a conceptual bio-physical BN (Figure 4.1, all nodes are nature nodes). The nodes of the BN are linked by conditional probability tables (CPTs) (Table 4.1). The states of the nodes and probabilities were based on general ecological knowledge and are illustrative in this conceptual model. The states and probabilities are model parameters that can be adjusted for case studies based on more quantitative data derived from the literature, fieldwork and experiments.

4.1.2 Management models

BNs can be an effective tool to communicate with stakeholders and present different management scenarios (Stewart-Koster et al., 2010).

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[3] *The peer reviewed BNs are available on the MadMacs website, and we will add additional models once they have been published: https://www.niva.no/en/projectweb/madmacs*

- Optimising decision from people's satisfaction

The decision for aquatic plant removal (e.g. mechanical harvesting) may depend on people's perception to mass development in relation to their activities (Figure 4.2). The decision of aquatic plant removal may be derived from mass development and people's satisfaction. Satisfaction is a utility node (Table 4.2). The value beside each decision choice in the decision node indicates the expected satisfaction (arbitrary unit) of making that choice and was calculated by multiplying the satisfaction of an event by the probability of that event. People's satisfaction could not be extracted directly from the surveys carried out as part of WP3.4 'Assessing the effects of aquatic weed removal on ecosystem service provision'. However, it is possible to derive it indirectly, similarly to what has been done now with people's perception of mass development.

- Scenario analyses balancing management costs and ecosystem valuation

Other management options (e.g. Hussner et al., 2017) may be explored, either alternatively or additively, to manage identified causes of mass development with knowledge of costs (Table 4.3), and in relation to ecosystem valuation (Table 4.4, Figure 4.3). The valuation of ecosystem services is greatly simplified in this conceptual diagram where the node 'activities' relate loosely to ecosystem services. This current BN is intended to link to WP3.4 'Assessing the effects of aquatic weed removal on ecosystem service provision' (e.g. Vermaat et al., 2016, Vermaat et al. in prep.).

Table 4.1: Conditional probability table linking resources and disturbances to mass development with illustrative probabilities. First two columns are the parent node states. Remaining columns are probabilities (%) of child node states conditional on parent node states.

		Probabilities (%) of mass development				
Resources	Disturbances	very low	low	medium	high	very high
low	low	0	0	30	40	30
low	moderate	50	50	0	0	0
low	high	100	0	0	0	0
moderate	low	0	0	0	50	50
moderate	moderate	0	0	100	0	0
moderate	high	50	50	0	0	0
high	low	0	0	0	0	100
high	moderate	0	0	0	50	50
high	high	30	40	30	0	0

Table 4.2: Utility table of the Satisfaction node in Figure 4.2 with illustrative values (arbitrary unit, e.g. relative happiness 0-100) as a function of two parent nodes: people's perception and decision for removal. Lowest satisfaction corresponds to decide to remove plants when perception is too little or not removing plants when perception is too much. Highest satisfaction is when there is a moderate amount of plants and no removal required.

People's perception	Decision for removal	Satisfaction
Too little	None	50
Too little	Partial	0
Too little	Full	0
Moderate	None	100
Moderate	Partial	80
Moderate	Full	40
Too much	None	0
Too much	Partial	50
Too much	Full	90

Table 4.3: Utility table of the Cost node in Figure 4.3 and Figure 4.4 with illustrative values (e.g. thousand €).

Management	Implementation cost
CO_2 supersaturation	-40
Nutrient removal	-50
Water level	-50
Peak flows	-100

Table 4.4: Utility table for the Value node in Figure 4.3 and Figure 4.4 with illustrative monetary values (same units as for the Cost node, thousand €).

People's desirability	Ecosystem valuation
Too little	50
Just right	100
Too much	-50

4.1.3 Consequences of macrophyte removal

This has proved to be the most challenging aspect to synthesise because the effects of plant removal are highly dependent on the context of the study (see Thiemer et al., 2021). Previous experimental studies of plant removal on ecosystem structure and functions were also based on individual elements or properties, not considering inter-linkages making the results idiosyncratic.

The effect of plant removal on ecosystem structure and functions has focused on a food web model (Figure 4.5), interconnecting many loose parts within an innovative framework including the type of system (standing water with floating or submerged plants, running water with submerged plants) and degree of plant removal (none, partial, full). A food web approach is proposed to investigate the short-term effect of plant removal on phytoplankton (Figure 4.5).

A systematic review has been published and includes all the details of the conceptual BN presented in Figure 4.5 (Thiemer et al., 2021). The BN is also available on the MadMacs web-site: https://www.niva.no/en/projectweb/madmacs

4.1.4 Quantifying people's perception

Thiemer et al. (in press) derived probabilities of people's perception of macrophyte mass development through a questionnaire (1234 respondents) and generalized linear mixed models (GLMMs). The state probability of the node **Perception** (Figure 6) were conditioned from the parent nodes Macrophyte species, Macrophyte growth form, Activity and Respondent type. Thiemer et al. then integrated this societal perspective (or cultural services) with the BN on the ecological consequences of macrophyte removal (Thiemer et al., 2021, Fig 4.6).

Note the conditional probability table linking people's Perception to Macrophyte removal (Figure 4.6) could not be quantified directly from the people's survey (an additional question would have been necessary), so Thiemer et al. (2021) assumed a simple inverse relationship between perception and macrophyte removal also dependent on macrophyte level of development (Table 4.5 and 4.6). Similar simple links can be developed to link people's perception to people satisfaction (see Section 4.1.2 above).

Table 4.5: Conditional probability table (in %) for macrophyte removal with respect to perception. Rational: inverse relationship. Based on Table 6. From Thiemer et al., 2022,

Perception	Macrophyte removal		
Nuisance	20	20	60
No nuisance	80	20	0

Macrophyte level	No nuisance			Nuisance		
1	0	0	0	0	0	1
2	0	0	0	0	1	1
3	0	0	0	1	1	1
4	0	0	1	1	1	1
5	0	1	1	1	1	1

4.1.5 Towards a global probabilistic model of causes of macrophyte mass development

Further to what was proposed in section 4.1.1, MadMacs needed to incorporate plant competition and the type of freshwater ecosystem to better characterise the causes of mass development with a global probabilistic approach. Plant competition is an important mechanism in standing waters, and involves competition between submerged and floating plants (Scheffer et al., 2003; Strange et al., 2019; Szabó et al., 2022). The way competition was incorporated into the BN is illustrated in Figure 4.7. Because standing and running waters may react differently to macrophyte removal, the type of freshwater ecosystem was incorporated as the degree of "water flow and substrate mobility" into Figure 4.7. The global quantitative functions linking resources to plant growth potential have been identified. Grazing effects are highly dependent on the specificity of the grazer, so it will be separated into different categories including generalist snail, crayfish, specialist (used in biological control). Water flow (water retention time) and substrate stability will allow to control the relative colonisation of submerged versus floating plants.

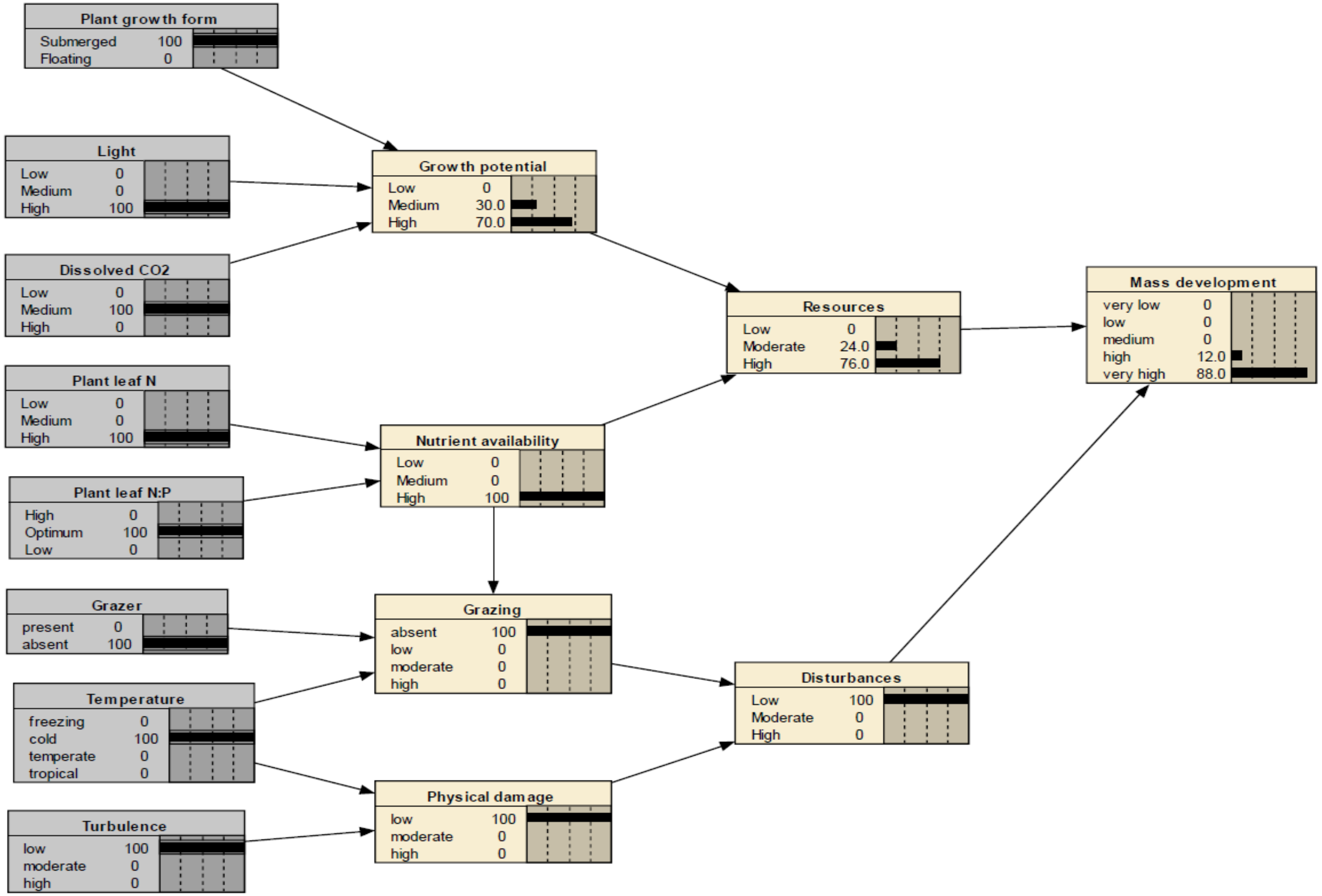

Figure 4.1: Mass development of aquatic plants. All nodes (boxes) were linked (arrows) with conditional probability tables (CPTs, see 4.Table 1 for an example). Individual nodes were characterised by their states (note low, medium, high may be changed to quantitative intervals). Knowing the state (or value) of the key causal variables (grey boxes), the BN can indicate the probabilities of mass development through the cascade of nodes and CPTs.

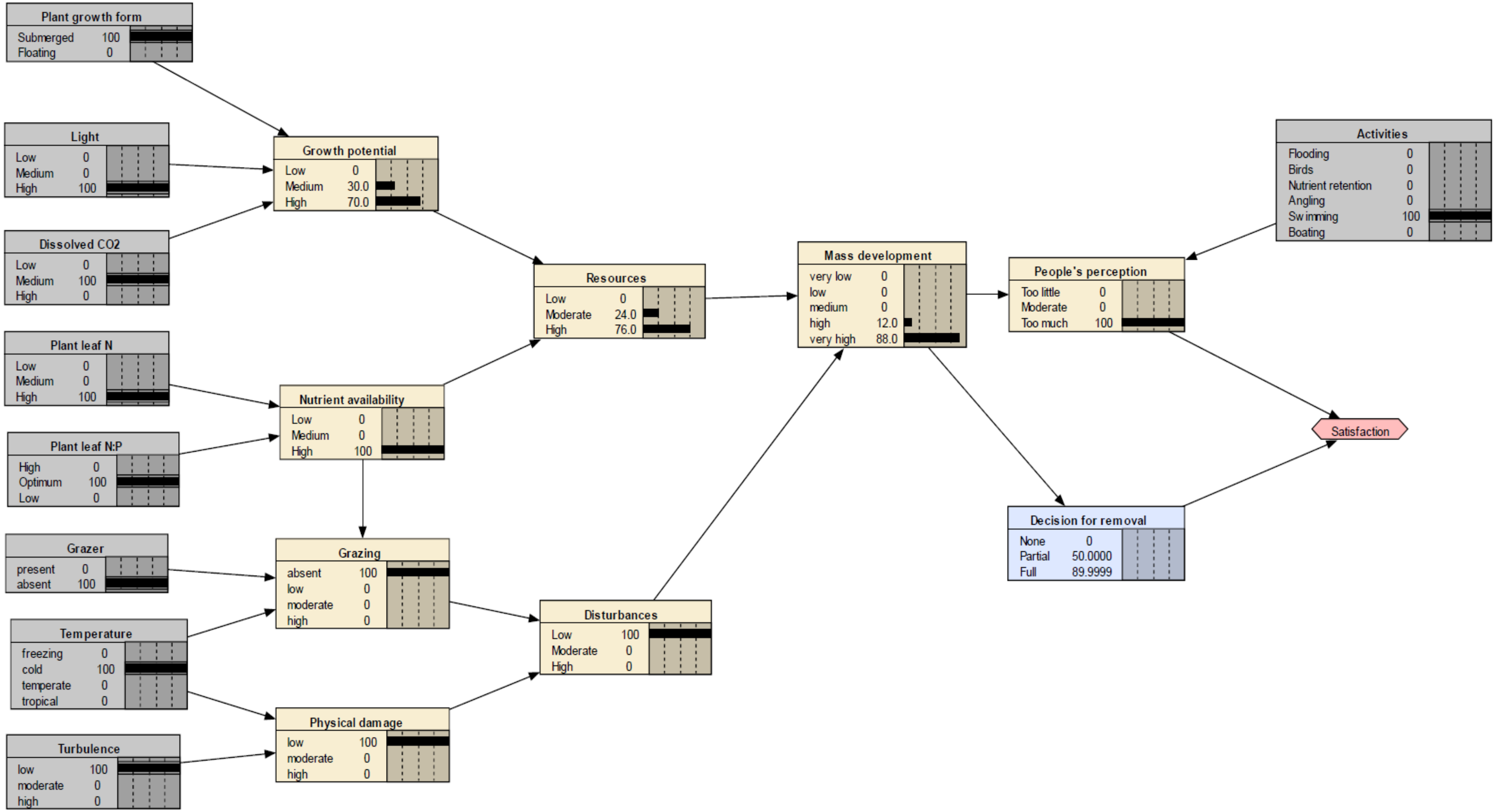

Figure 4.2: Same as Figure 4.1 with additional decision node (purple box) for aquatic plant removal conditional on people's perception related to their activities (e.g. swimming, possible to choose a range of activities) and satisfaction node (pink hexagon, Table 4.2). The value beside each decision choice (purple box) indicates the expected satisfaction (here range 0-100) of making that choice. In this instance, full removal provides the highest satisfaction.

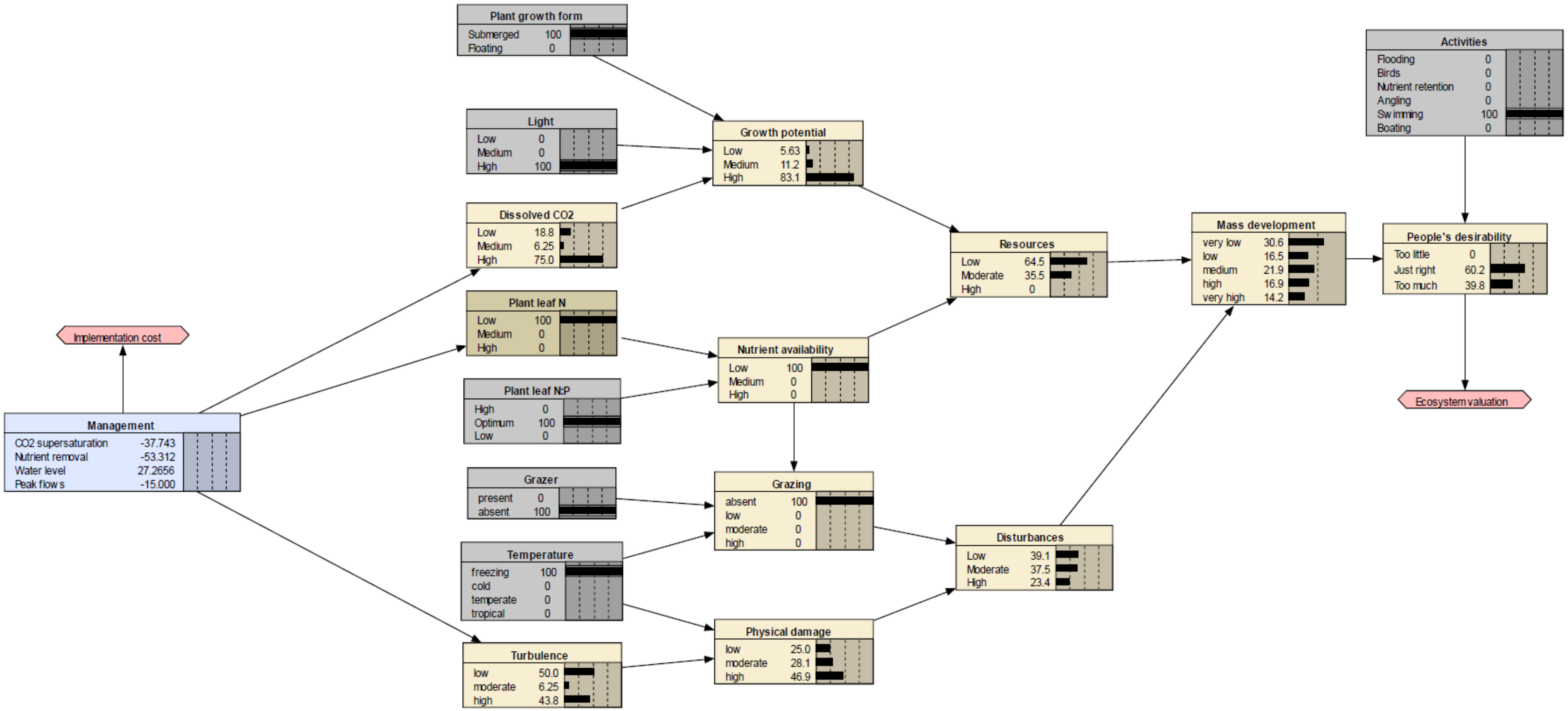

Figure 4.3: Similar to Figure 4.1 and Figure 4.2, this time the decision node (purple box) represents different management strategies to change key causal variables. Management decision is derived from balancing cost of management implementation (pink hexagon, Table 4.3) with ecosystem valuation (pink hexagon, Table 4.4) in relation to people's desirability of mass development linked to activities (e.g. swimming). Values in the Management decision node represent the balance between costs and likelihood of ecosystem valuation based on people's perception of mass development for different activities (e.g. swimming). Management of water level is the only one bringing benefits, so we select it and observe how the probabilities are affected throughout the BN (see Figure 4.4). Note nutrient removal was ineffective in this case as we defined a nutrient poor environment (low Plant leaf N) for all management options.

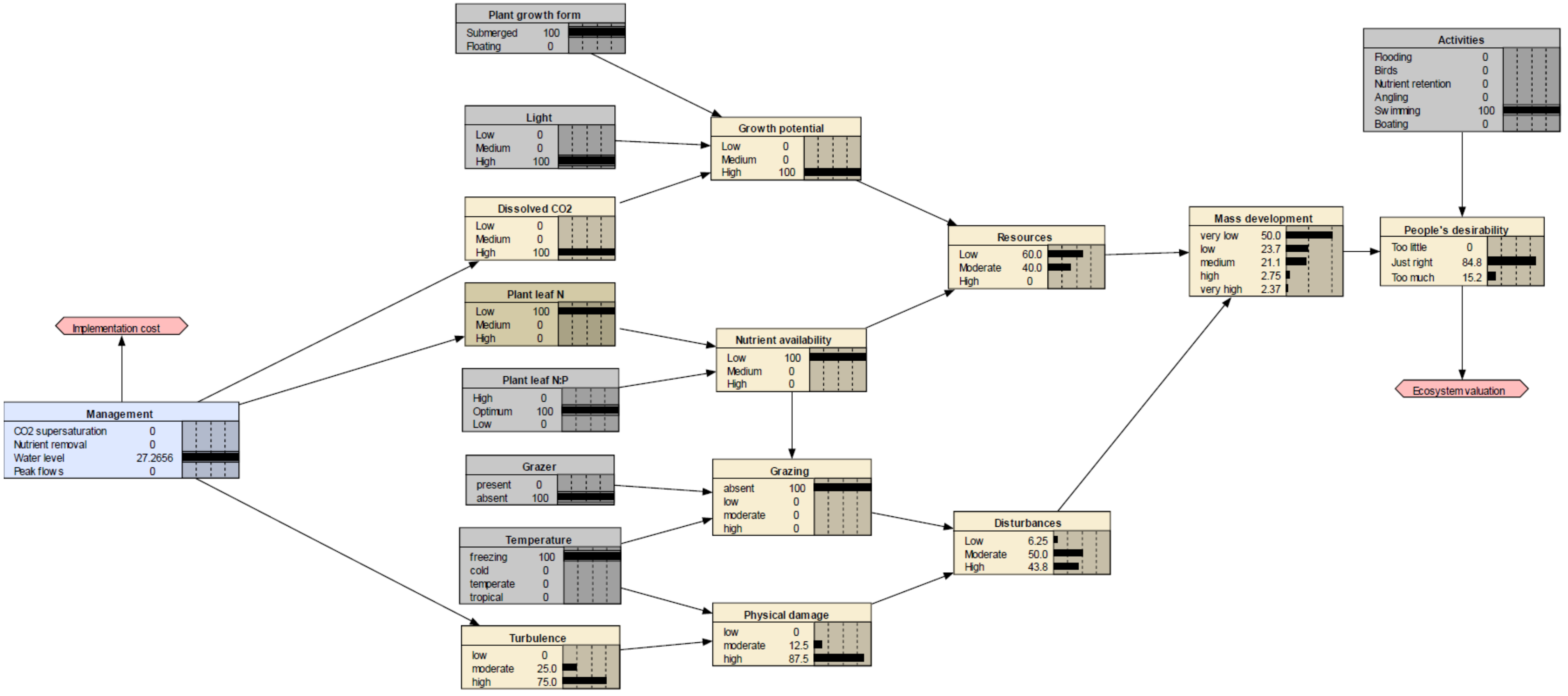

Figure 4.4: Same as Figure 4.3, after choosing Water level management as the best option with an added value of 27 thousand €. This single management brings probabilities of mass development to 'very low' (50%) and 'low' (24%) and people's desirability to 'just right' (85%) linked to the highest ecosystem valuation. Compare with Fig 4.3. Management of peak flows also produced similar probabilities, but its implementation cost was double the management of water level. The reduction of CO_2 supersaturation and nutrient removal were comparatively ineffective.

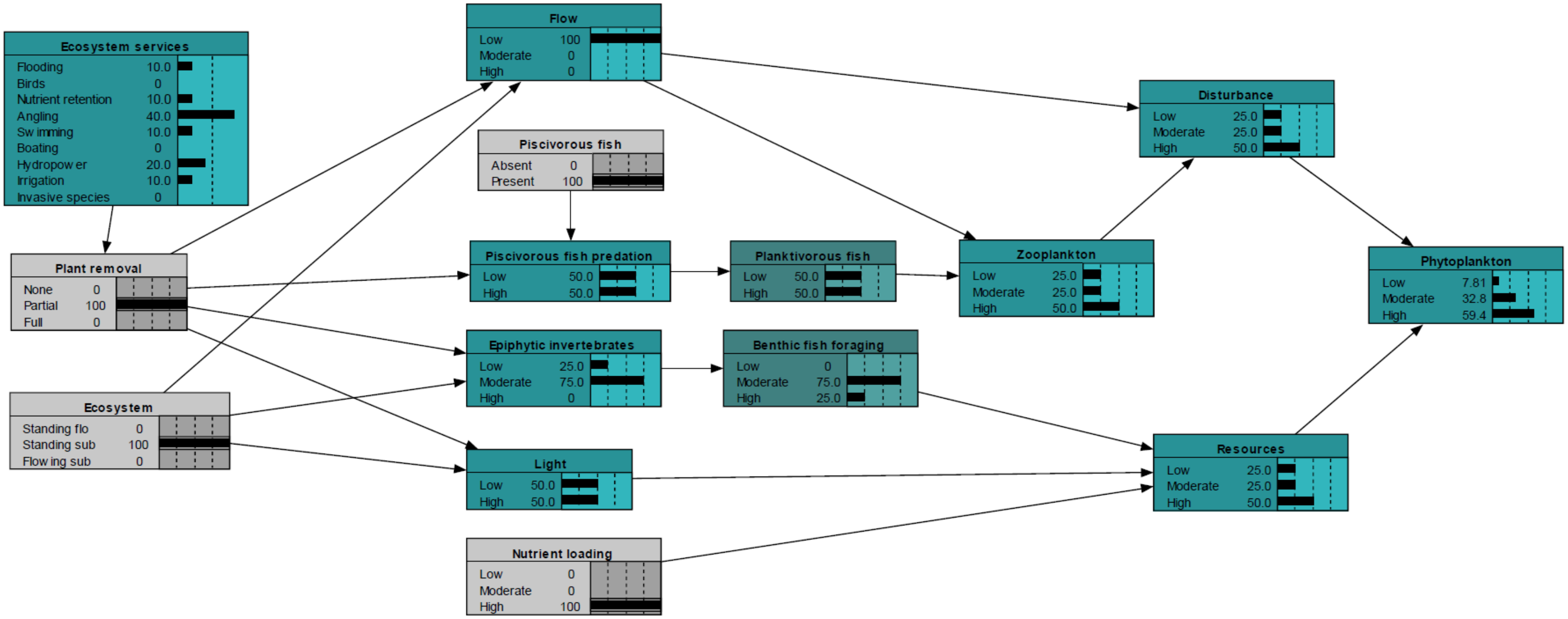

Figure 4.5: Effects of plant removal on ecosystem structure with phytoplankton as the endpoint. Results were conditional on partial plant removal, standing water with submerged plants, presence of piscivorous fish and high nutrient loads (grey nodes). Plant removal may be conditioned by ecosystem services. A decision node could be added as in Figure 4.3 and 4.4. From Thiemer et al., 2021.

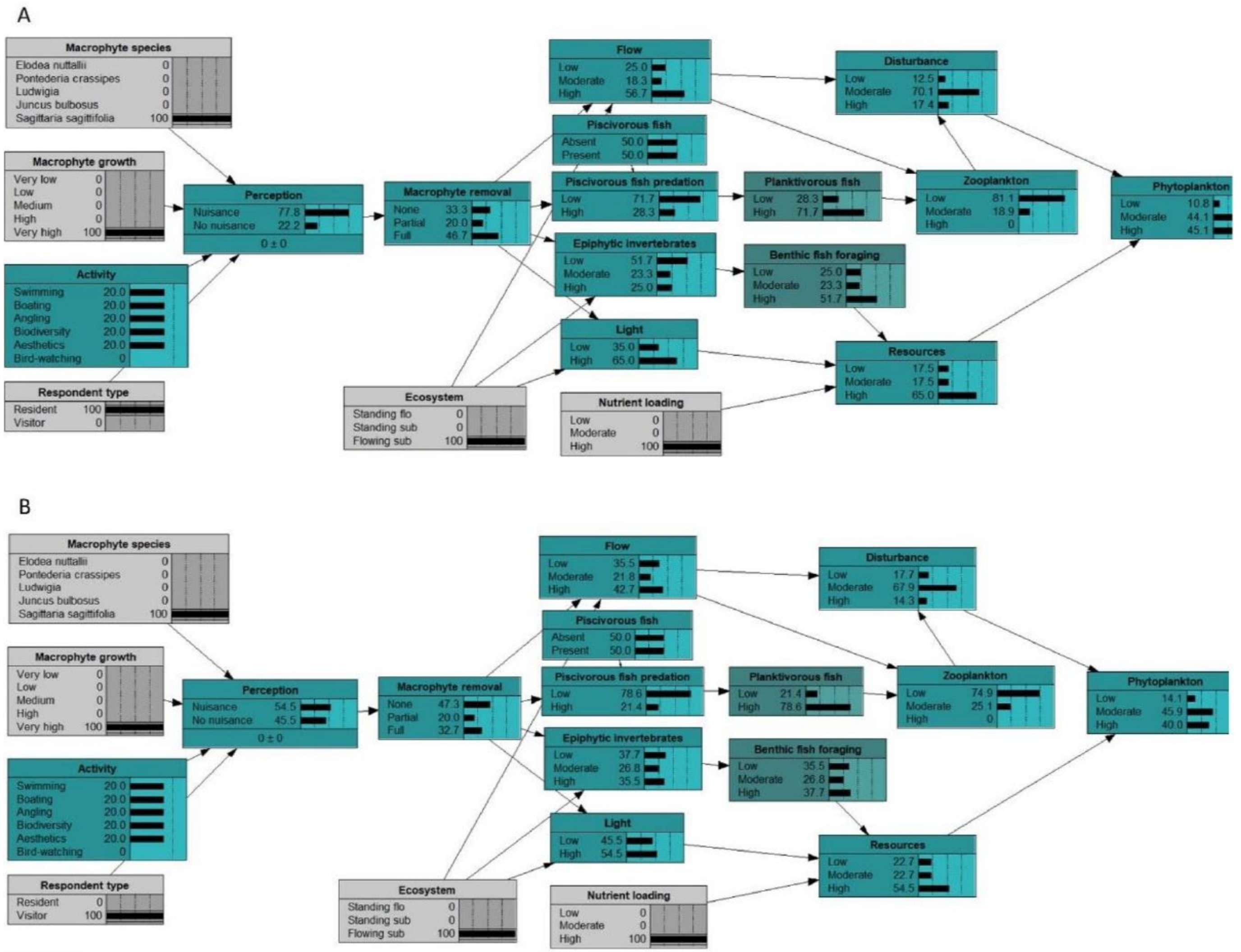

Figure 4.6: BNs of probability of management alternatives for a riverine system with high nutrient loading and very high *Sagittaria sagittifolia* growth A) Probabilities for respondent type is set to resident B) Probabilities for respondent type is set to visitors. Grey boxes indicate nodes that have been specified. From Thiemer et al., 2022.

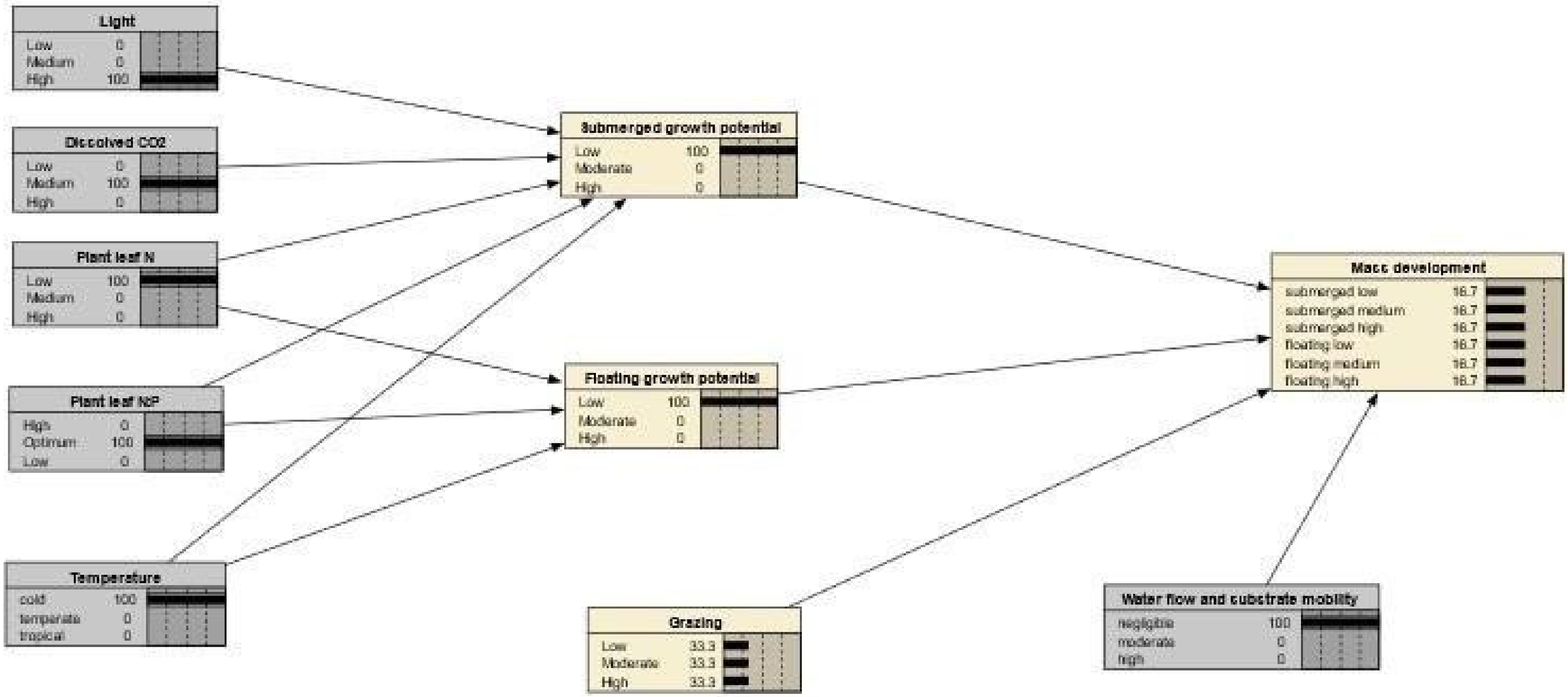

Figure 4.7: Revisiting the BN causes of mass development of aquatic plants (BN in construction with quantitative probabilities).

CHAPTER 5: INTEGRATING AQUATIC PLANT NUISANCE PERCEPTION INTO A PROBABILISTIC MANAGEMENT DECISION TOOL[4]

5.1 INTRODUCTION

Freshwater ecosystems make up only 0.01% of the world's water (Dudgeon et al., 2005), yet this small fraction constitutes highly valuable natural resources from which human societies receive important ecosystem services (i.e. human benefits obtained from nature) (Janssen et al., 2021). Aquatic macrophytes are considered vital in freshwater ecosystems as their presence influences both physical, chemical and biological characteristics of aquatic ecosystems (Jeppesen et al., 1998) and consequently, a series of ecosystem services (Grizzetti et al., 2016; Janssen et al., 2021; Millennium Ecosystem Assessment, 2005). Ecosystem services provided by macrophytes include supporting (habitats for periphyton, invertebrates and fish), provisioning (food, fertiliser, biomass fuel), regulating (carbon sequestration, nutrient retention, water purification, pest and disease control) and cultural services (recreation activities, appreciation of landscape and appreciation of biodiversity non-use) (Boerema et al., 2014; Janssen et al., 2021). The societal benefits that macrophytes provide may, however, be diminished when macrophytes occur at high densities (i.e. mass development), as macrophytes are often perceived a nuisance when they impede drainage (Baattrup-Pedersen et al., 2018), irrigation (Armellina et al., 1996) or recreational activities (Verhofstad and Bakker, 2019).

In freshwater ecosystems, solutions to combat this perceived nuisance growth include mechanical removal (cutting and dredging), chemical control (herbicides) and biological control (herbivorous fish, manatees or insects), where mechanical removal is the most common management practice in the Northern hemisphere (Hilt et al., 2006; Vereecken et al., 2006; Verhofstad and Bakker, 2019). Mechanical macrophyte removal may eliminate nuisance macrophyte growth and thereby reduce the interference of macrophytes with human activities (Verhofstad and Bakker, 2019). At the same time, ecosystem services such as good water quality depend on the structure and functions provided by macrophytes. Freshwater managers should therefore seek to reach a macrophyte growth level that maximises the total ecosystem services value (Janssen et al., 2021). Bayesian networks (BNs) have previously been used by water managers as a decision support tool (Langmead et al., 2009; Stewart-Koster et al., 2010), and may be useful to integrate different user groups' perceptions of macrophyte growth and the consequences of macrophyte removal on ecosystem properties, assisting water managers in optimizing their strategies. In addition, BNs can be an effective tool to communicate with stakeholders and present different management scenarios (Stewart-Koster et al., 2010). Water managers need information on the consequences of different removal alternatives and information on when macrophytes become a nuisance to optimise the management of ecosystems with mass

[4] Thiemer, K, Immerzeel, B, Schneider, S, Sebola, K, Coetzee, J, Baldo, M, Thiebaut G, Hilt, S, Köhler, J, Harpenslager, S-F, Vermaat, J.E. 2022. Integrating aquatic plant nuisance perception into a probabilistic management decision tool. Environmental Management, in press.

developments, where BNs can be used as a decision support tool. Many individual studies have quantified the consequences of macrophytes removal (reviewed by Thiemer et al. (2021), yet studies investigating when macrophytes become a nuisance are few (Kuiper et al., 2017; Verhofstad and Bakker, 2019).

Nuisance growth of macrophytes has been regularly reported in scientific reports and popular media (Pieterse and Murphy, 1990; Verhofstad and Bakker, 2019), but to our knowledge, only a single attempt has been made to quantify at what extent submerged macrophytes become a nuisance for specific cultural ecosystem services (Verhofstad and Bakker, 2019), while nuisance from free-floating and emergent macrophyte life-forms remains mostly unexplored. Perception of macrophytes as nuisance is likely to depend on different parameters such as the spatial extent of the vegetation, the species (including the notion of invasiveness), plant life-form (submerged, free-floating or emergent), type of activity (swimming, boating, angling, etc.) and socio-demographic parameters (resident/visitor, environmental-mindedness). Correspondingly, Verhofstad & Bakker (2019) concluded that creating a single threshold for cover and clear water depth above the macrophyte canopy is impossible and that classification of nuisance levels will benefit from including site-specific information on the perception of nuisance.

Building on this lack of quantitative data, we explored the level at which macrophytes are perceived as nuisance and the patterns in underlying drivers. A survey was conducted among resident and visitors in all five study sites that had the same design, length and set of questions but differed in the specification of the local macrophyte mass development problem (Table 1). The study expected to find that: i) higher abundance or cover of macrophytes will cause a higher probability of perceived nuisance; ii) nuisance thresholds vary between respondent type (resident and visitor), where residents may perceive macrophytes as nuisance at lower levels, due to their *a priori* knowledge of the nuisance issue and removal practices at the given site, which visitors do not necessarily have; iii) respondents with higher environmental mindedness will consider macrophyte growth less of a nuisance; and iv) nuisance thresholds are influenced by respondent activities, where perceived nuisance is likely to be higher for recreational activities such as swimming, boating and angling compared to appreciation of biodiversity, appreciation of landscape and birdwatching. The BN of Thiemer et al. (2021) was expanded to integrate user perceptions of mass developments with the possible effects of different management options. This will provide a management decision support tool that can optimise the management of ecosystems with macrophyte mass developments.

5.2 METHODS

5.2.1 Perception of macrophyte growth

Surveys were used to obtain data on people's perceptions of macrophyte growth in relation to different user activities in five different study sites: Lake Kemnade in Germany dominated by invasive *Elodea nuttallii* ((Planch) St. John), Hartbeespoort Dam in South Africa dominated by invasive *Pontederia crassipes* (Mart.), Lake Grand-Lieu in France dominated by invasive *Ludwigia* species, River Otra in Norway dominated by the native *Juncus bulbosus* (L.) and River Spree in Germany dominated by several native macrophytes (mainly *Sagittaria sagittifolia* (L.)).

The surveys had a common structure (see Supplementary Information 1 for an example) but were adjusted to local conditions (i.e. swimming is not allowed in Lake Kemnade and Lake Grand-Lieu, and birdwatching was included as a separate activity only in Grand-Lieu). To classify the perception of macrophyte growth, respondents were asked to choose level(s) of macrophyte growth (ranging from 1-5) that they considered a nuisance (Figure 5.1, i.e. not ticking a level was considered as answering not a nuisance). In addition, respondents were asked to distribute 100 points across 4-5 activities (swimming, boating, angling, appreciation of biodiversity, birdwatching, and appreciation of landscape) as an indicator of the importance of each of these activities for the individual respondent. The last part of the survey covered a sequence of questions on general social-demographic information including age and gender that was used to give context. Validation of sample representativeness was not performed, as these surveys were not designed to represent the whole population. Questions on what the respondents' decisions on levels for nuisance were based were included, as well as a standard set of questions targeting a respondent's opinion on environmental issues. For this purpose, the New Environmental Paradigm Scale (hereafter NEP-score) was included, which has been developed to estimate the environmental-mindedness of the respondents' worldview (Dunlap, 2008; Dunlap et al., 2000; Dunlap and Van Liere, 1978). To calculate the NEP, the respondents were presented a series of statements that either support an anthropogenic or ecocentric world view (Immerzeel et al., 2022) and respondents rated to what degree they agreed on the statements on a scale from "strongly disagree" to "strongly agree". An example of the surveys from the River Otra can be retrieved in Supplementary Information 1.

5.2.2 Data collection

Prior to data collection, the surveys were translated into local language by native speakers. An English version was used for respondents not speaking the local language. The surveys were qualitatively pre-tested twice for each study site. Pre-testing included a variety of scientists (not involved in this study) reading through and commenting on the survey, and we also distributed the surveys among friends and families to do the same. A second round of pre-testing with the same pre-testers was performed after including the suggestions received from the first pre-testing round. Quantitative pre-testing on a sub-sample of the population, as suggested by Johnston et al. (2017), was not possible, due to the limited time budget and the large geographic spread of the study sites.

The surveys for the five study sites were collected using both an online version and a printed version. This combination helped in achieving the required sample size and likely enhanced representativeness by covering a broader suite of respondents, as using only face-to-face collected surveys could introduce a sampling bias (Lindhjem and Navrud, 2011). The online versions were distributed via e-mail lists, social media, websites for local organisations and hand-out QR codes, whereas the printed version was collected on-site from face-to-face encounters and pick-up and drop-off places. At each study site, 2-6 surveyors visited the area and distributed printed surveys among respondents at local recreation hotspots, shops, museums, tourist visitor centres and other public areas. Surveys were collected in Hartbeespoort Dam in January 2020, River Otra June-September 2020, River Spree June-August 2020, Lake Grand-Lieu July-August 2020 and Lake Kemnade July-August 2020. The face-to-face collection of the printed surveys was done in accordance with the COVID-19 restrictions prevalent at the given time for each site. The surveys were anonymous and complied with the data protection and privacy rules in the given country.

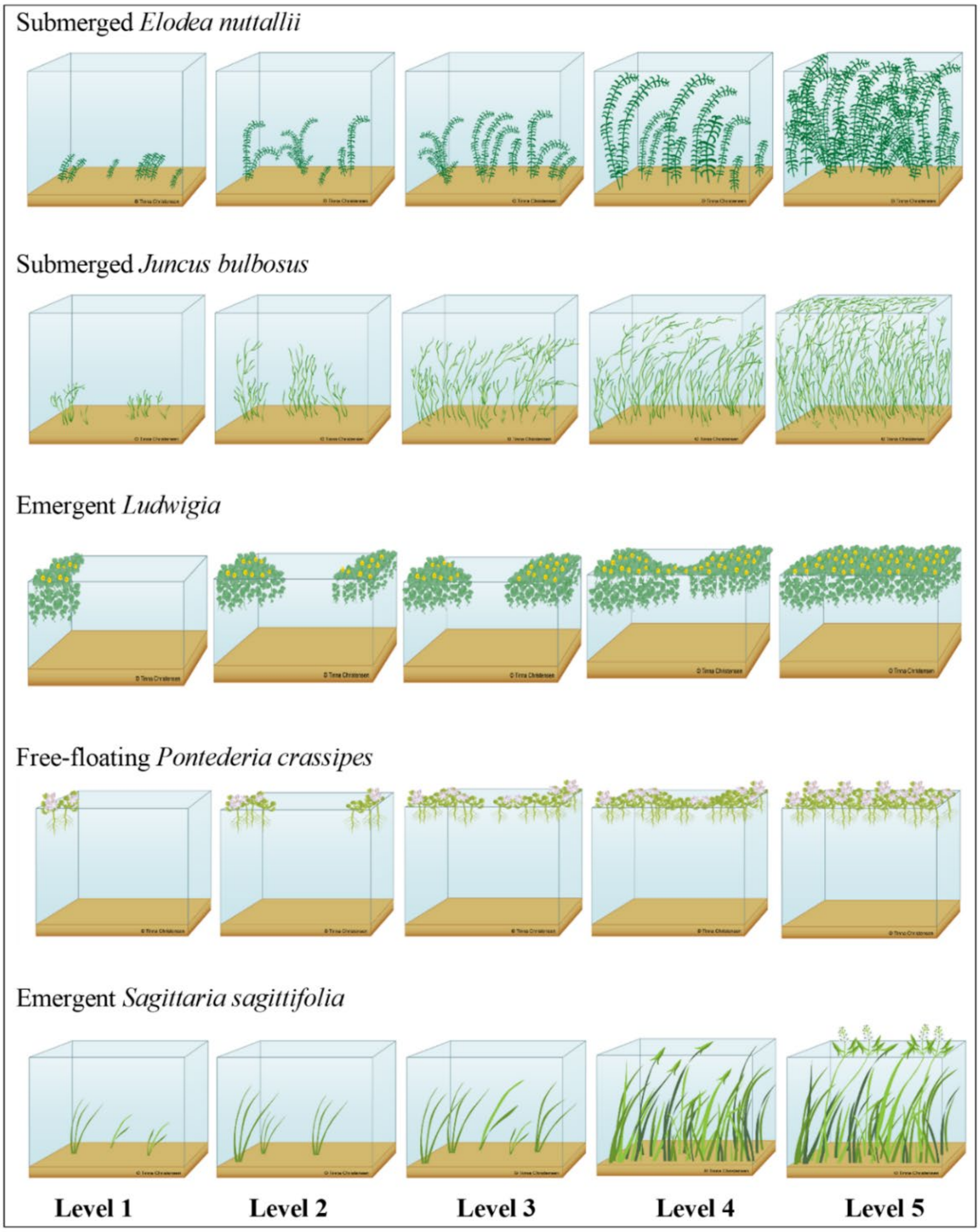

Figure 5.1: Pictures used in the survey question assessing the perceived nuisance level for each of the five macrophytes species. The five study sites were Lake Kemnade in Germany dominated by the invasive *Elodea nuttallii*, the River Otra in Norway dominated by the native *Juncus bulbosus*, Lake Grand-Lieu in France dominated by invasive *Ludwigia* species, Hartbeespoort Dam in South Africa dominated by invasive *Pontederia crassipes,* and the River Spree in Germany dominated by several native macrophytes (mainly *Sagittaria sagittifolia*).

5.2.2.1 Data preparation

Survey data are prone to various types of selection bias (Johnston et al., 2017), thus prior to the analyses we checked the survey data, by removing non-response answers and inaccurate or clearly inconsistent ‘protest’ answers (for example, distributing more than 100 points when asked to distribute 100 points). We used a conservative strategy to remove responses and only included respondents that filled out the willingness to pay questions (same criterion is used in Vermaat et al. in prep.). Consequently, between 58 and 89% of the collected surveys could be used, depending on the case study site. The question regarding perceived nuisance was mistranslated for the survey on *Ludwigia*, where respondents were asked to indicate the lowest level at which they perceived the growth a nuisance, hence leaving higher levels unticked. The answers were adjusted for these respondents by giving all above levels from the ticked level the value 1 (i.e. nuisance). Furthermore, the ecological mindedness, i.e. the NEP-score, was calculated for each respondent by transforming the responses “Strongly disagree” to “Strongly agree” into a 1-5 scale and then calculating the arithmetic mean across all the questions, as described in Dunlap et al. (2000). A low NEP-score means a more anthropogenic worldview whereas a larger NEP-score a more ecocentric worldview.

5.2.3 Data analyses

All statistical analyses were made in R version 3.6.4 (R Core Team, 2020) using the following packages: lme4 (Bates et al., 2021), emmeans (Lenth et al., 2022) and MASS (Ripley et al., 2021). Graphics were made using the R package ggplot2 (Wickham et al., 2020). The Bayesian networks were built using the NETICA software v. 6.07 (Norsys, 2005).

5.2.3.1 Perception of macrophyte growth

Perception of macrophyte growth (i.e. probability of perceiving growth as a nuisance) was analysed using generalized linear mixed models (GLMMs) with a binomial family (log-link). Each macrophyte species was analysed separately, as the macrophyte growth levels (pictures 1-5 from surveys, used as continuous predictor, Figure 5.1) only correspond qualitatively among the species, but do not reflect the same absolute biomass or plant density.

Initially, the influence of macrophyte growth level (1-5), respondent type (resident, visitor) and ecological mindedness of respondents (NEP-score) on the probability of perceiving macrophytes as a nuisance (0 or 1) were examined. Candidate models with the interaction between respondent type and macrophyte growth level were compared to models without the interaction using Akaike information criteria (AIC), in which the most strongly supported model has the lowest AIC (Anderson, 2007). When the difference in AIC among two models (delta AIC) was lower than 2, the simplest model was chosen (Burnham and Anderson, 2004). Respondent IDs were set as a random effect to account for the lack of independence of observations made by each respondent. Macrophyte growth levels at which the probability for perceived nuisance was 50%, hereafter called median nuisance levels, were estimated using the *dose.p* function from the MASS package (Ripley et al., 2021).

To understand how macrophyte growth is perceived by respondents when engaged in different activities, the influence of activity (swimming, boating, angling, appreciation of biodiversity, appreciation of landscape and birdwatching) on the probability of nuisance were tested using GLMMs with a binomial family (log-link) for the five macrophyte species separately, as not all activities were possible for the respondents at the respective site. Interaction between activity and respondent type, activity and macrophyte growth, respondent type and macrophyte growth were tested by comparing candidate models with and without these interactions and selecting the model with the lowest AIC (Anderson, 2007). Moreover, all observations (Nuisance 0 or 1) were weighted by the proportion of the 100 points from the question on the importance of activities for each respondent, to differentiate between respondents with a clear preference for one activity, and respondents with a more "casual" use of the ecosystem for several activities.

5.2.3.2 Decision support tool for water managers using Bayesian network approach

Managing ecosystems with macrophyte mass developments may involve balancing people's perception and consequences of removal for the ecosystem. A Bayesian network is a model based on probabilities: it can be constructed from a system of boxes (parent and child nodes) connected by arrows that represent conditional dependencies, each with a probability, between the nodes (Steward-Koster et al., 2010). The network is quantified by conditional probability tables (CPTs) for each child node that can be quantified either by observational data or expert knowledge (Korb and Nicholson, 2004; Pollino et al., 2007). Here we use the BN approach as a first attempt to build a decision support tool for water managers in charge of ecosystems with macrophyte mass developments, by integrating people's perceptions of macrophytes and the short-term consequences of mechanical macrophyte removal. Water managers can manipulate the BN to quantify this risk under different scenarios, e.g. to simulate the effects on alternative desirable ecosystem services. The CPTs in the BNs are based on empirical perception patterns from the surveys (probabilities of nuisance for combinations of respondent type, activity, macrophyte species and macrophyte growth levels) and are here integrated with an existing BN on short-term consequences of mechanical removal developed by Thiemer et al. (2021). A detailed description of this existing network can be found in Thiemer et al. (2021) and in Supplementary Information 2.

5.2.3.3 Description of the decision support tool (Bayesian network)

In the part of the BN quantifying people's perception of macrophyte growth (Figure 5.2), *Perception* is a function of four predictor variables *Activity* (swimming, boating, angling, appreciation of biodiversity, appreciation of landscape, birdwatching), *Respondent type* (resident, visitor), *Macrophyte species* (*E. nuttallii, P. crassipes, Ludwigia* spp., *J. bulbosus, S. sagittifolia*) and *Macrophyte growth level* (1-5) which are all likely to influence the perception of people. Since environmental mindedness was not significant in the GLMM analyses, we left it out of the model. *Plant management option* indicates the proportion of macrophyte removal (none, partial or full). *Plant management option* links the *People's perception* with the BN on short-term consequences of macrophyte removal developed by Thiemer et al. (2021). In short, this part of the BN illustrates the short-term effect of macrophyte removal on ecosystem structure with a focus on a food web model (*Phytoplankton* as end-point), because one major consequence of cutting aquatic plants is the increased risk of phytoplankton blooms (Kuiper et al., 2017). *Phytoplankton* growth is controlled by *resources (Light* and *Nutrient availability)* and *disturbances* (*Flow* and *Trophic cascade*) (Bernes et al., 2015; Reynolds, 2000) and can be adjusted to local conditions changing the nodes *Ecosystem* and *Nutrient loading*. In this BN, water managers can either set the risk of a phytoplankton bloom (endpoint) to a specific target and see how probabilities are affected backwards throughout the whole BN, identifying key nodes on which the set target depends, or set the target group of people (e.g. residents angle) and see which management alternative is recommended and what the consequences for the ecosystem will be. Finally, setting both a target for a specific user group and for ecosystem properties is possible with the BN. This will allow for a systematic evaluation of management alternatives.

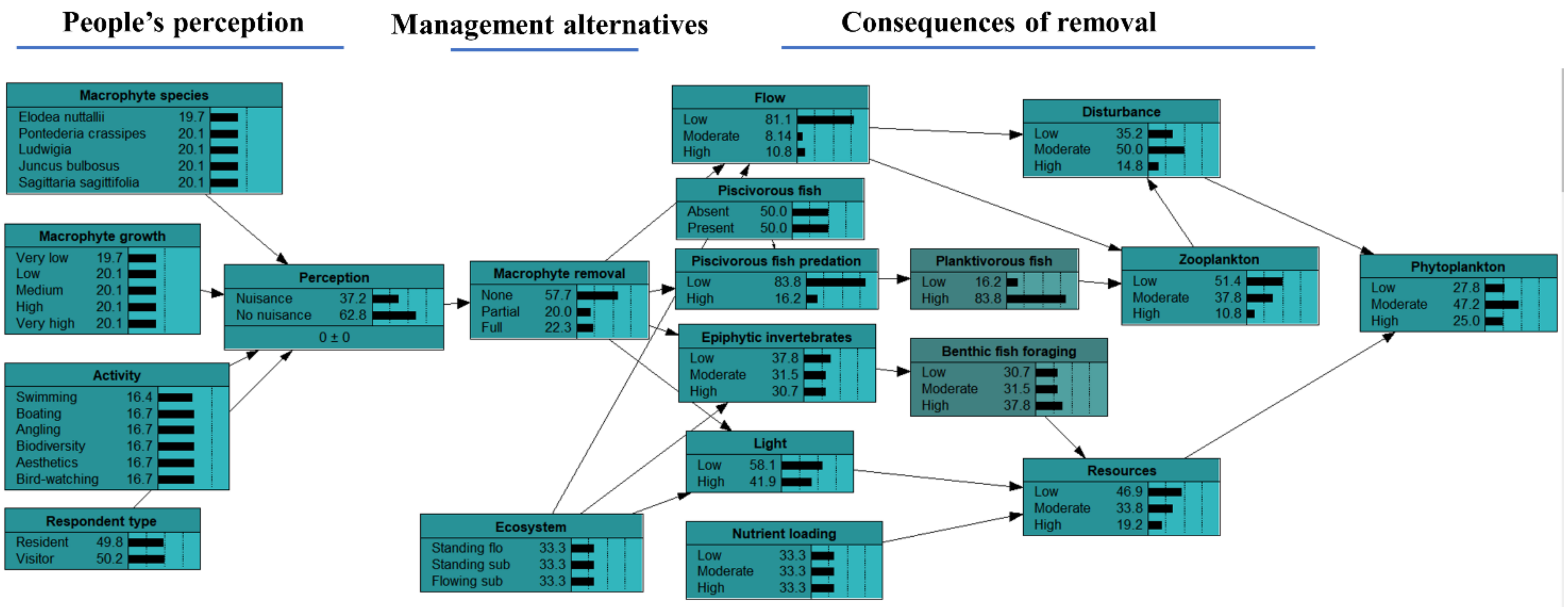

Figure 5.2: BN integrating people's perception of macrophyte growth, consequences of macrophyte removal and potential management alternatives. All nodes were linked with conditional probability tables (Supplementary Information 2). Nodes were characterised by their states (1-5). The BN component on perception builds on the currently presented survey data whereas the component on consequences is taken from Thiemer et al. (2021) where CPTs were based on expert knowledge derived from the literature.

5.3 RESULTS

5.3.1 Perception of macrophyte growth

A total of 1,234 survey responses were retained after quality control and analysed, with sample sizes varying between 167-304 for the five study areas (Table 5.1). Overall, the fraction of respondents considering at least one of the macrophyte growth levels a nuisance was high, ranging from 70-99% and 66-95% for residents and visitors, respectively, across the five sites (Figure 4.3). The fraction of respondents answering "I don't know" was higher for visitors (2-34%) than for residents (1-8%, Figure 5.3).

For all macrophyte species, the probability that macrophytes were perceived as a nuisance increased with macrophyte growth level (Figure 5.4. *E. nuttallii* and *S. sagittifolia* had considerably lower probabilities for perceived nuisance at low macrophyte growth levels (< 3) than the other three species (Figure5.4). A comparison of the median perceived nuisance levels among the five species (Figure 4) shows that *Ludwigia* spp. (3.1 ± 0.1 SD) and *P. crassipes* (3.2 ± 0.1 SD) were considered a nuisance already at low levels followed by *J. bulbosus* (3.6 ± 0.1 SD), *E. nuttallii* (4.1 ± 0.1 SD) and *S. sagittifolia* (4.3 ± 0.1 SD). Visitors generally had a lower probability of considering growth of *E. nuttallii* and *J. bulbosus* a nuisance than residents (Figure 5.4). This difference in probability was 24% for *J. bulbosus* and 10% for *E. nuttallii,* respectively. Visitors' and residents' perception did not differ for *Ludwigia* (Figure 5.4). Interestingly, for *S. sagittifolia* and *P. crassipes* the interaction between respondent type and macrophyte growth level was significant. This suggests that the increase in probability for nuisance with increasing macrophyte growth was not the same for visitors and residents. For *S. sagittifolia,* the two probability curves are parallel at lower plant levels but start to deviate at higher plant levels, whereas the opposite was found for *P. crassipes* (Figure 5.4). Finally, the environmental mindedness of the respondents (NEP-score) did not influence the perception of macrophytes as a nuisance (GLMMs).

5.3.1.1 Perception of macrophyte growth among different activities

Preferred activities of individual respondents were obtained from the question where respondents could distribute 100 points among four to six (dependent on the study site) activities. This distribution of points revealed that most respondents were engaged in more than one activity and only few respondents gave all 100 points to a single activity (Figure 5.5).

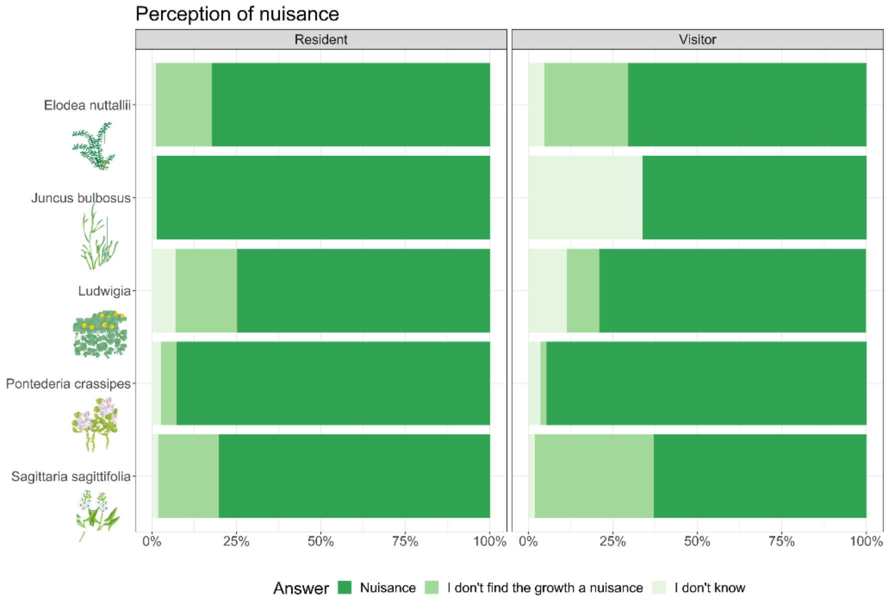

Figure 5.3: Fractions (%) of residents and visitors that have answered either that the one or more of the macrophyte growth levels were a nuisance, do not think it is a nuisance or do not know in each of the five cases.

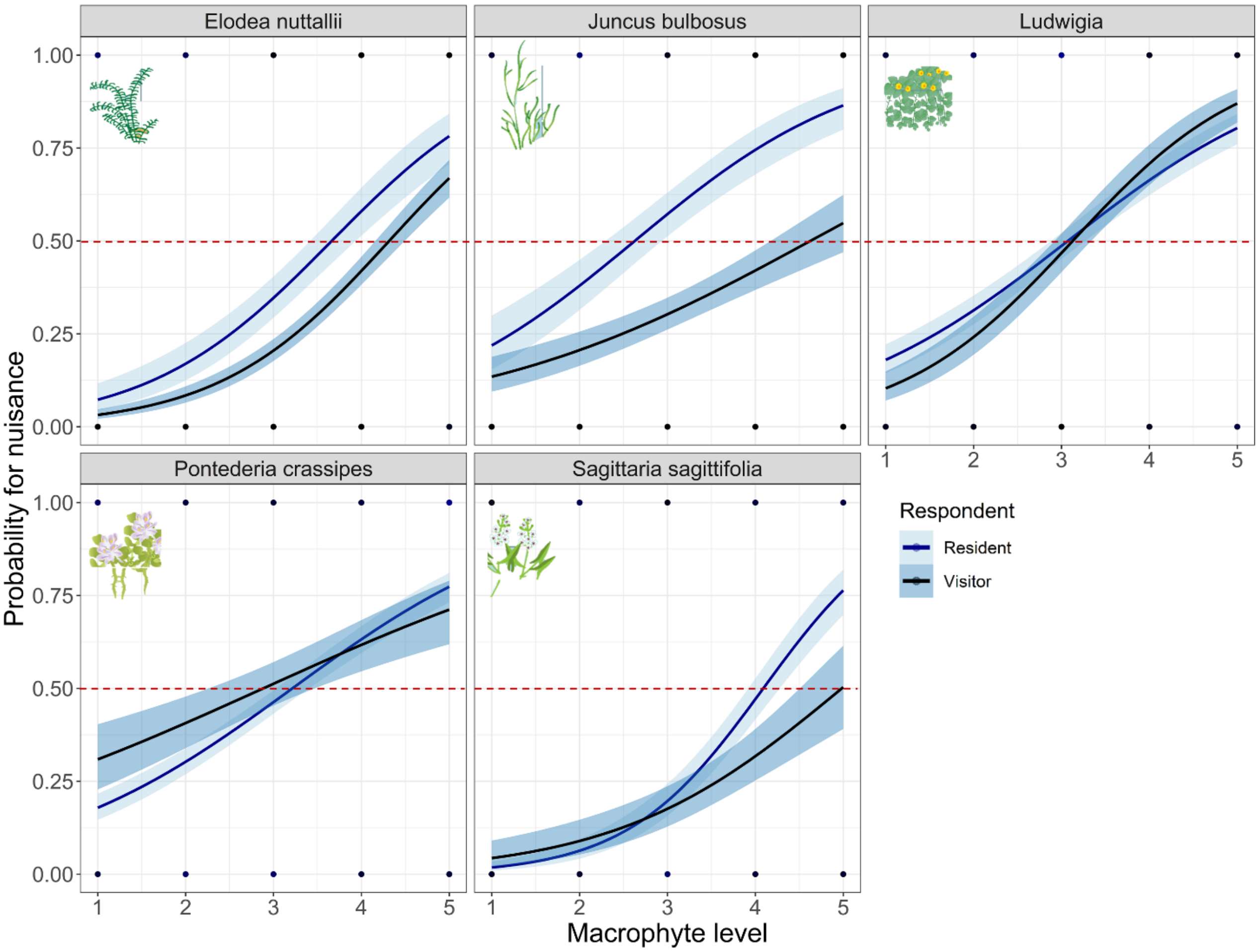

Figure 5.4: Probability of perceived nuisance in relation to macrophyte growth level (1-5), macrophyte species and respondent types (resident and visitor) (GLMMs). Bands are confidence intervals (0.95). The red dashed line represents the level at which probability of nuisance is 50%.

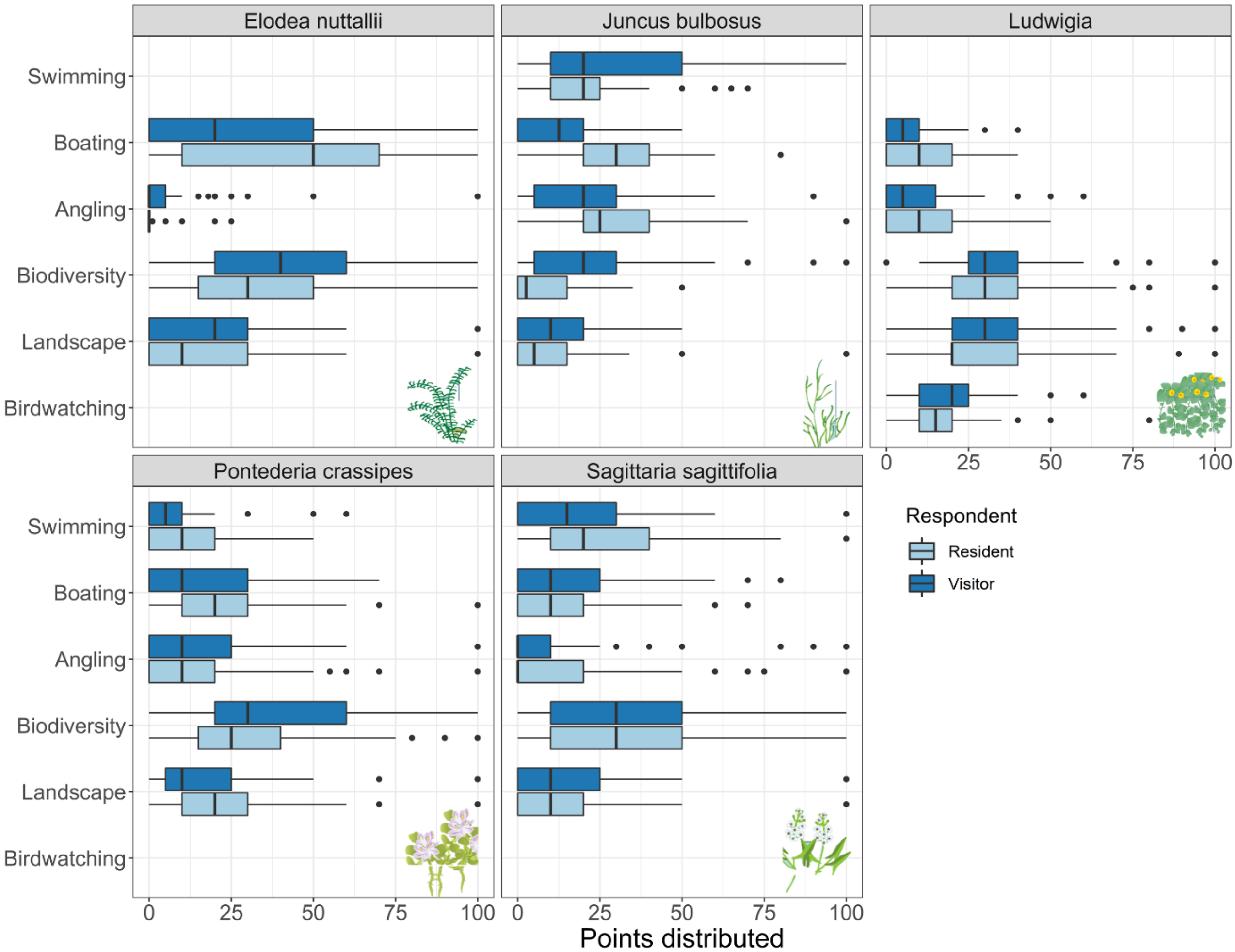

Figure 5.5: The distribution of points (0-100) given by respondents to different activities at the five sites characterised by different macrophyte species (for residents and visitors, respectively). Vertical bold lines indicate the median, boxes the 25% and 75% percentiles, and whiskers the minimum and maximum values.

Overall, the activity type had a significant effect on the level of perceived nuisance, yet macrophyte growth level, respondent type and their interaction explained most variation in perceived nuisance (Figure 5.6). Different patterns in probability for perceived nuisance in relation to preferred activity were found for the five macrophyte species, regardless of their interaction with respondent type and the interaction of respondent type and macrophyte growth level (Figure 5.6A-F). The probability of perceiving the submerged *J. bulbosus* growth as a nuisance was in general high for all activities (i.e. user groups), yet the probability of perceived nuisance was 41% (±15%, SE) higher for respondents who stated swimming as an important activity compared to respondents stating that appreciation of landscape was important, when controlling for all other variables (Figure 5.6). Probability for perceived nuisance was likewise high for the free-floating *P. crassipes,* but in contrast to *J. bulbosus* the probability for perceived nuisance was found to be 7% (± 5%, SE) less likely for respondents stating swimming as an important activity compared to appreciation of landscape (GLMM, $P<0.001$). For the submerged *E. nuttallii* in Lake Kemnade the probability of perceived nuisance was 31% (±6%, SE) higher for respondents who stated boating as important compared to appreciation of landscape (GLMM, $P<0.001$), whereas perceived nuisance of *S. sagittifolia* in the Spree was 14% (±9%, SE) less likely for respondents stating that appreciation of biodiversity as an important activity compared to appreciation of landscape. Finally, a significant interaction of respondent type and activity was found for *P. crassipes*, suggesting that visitors and residents did not equally consider growth of *P. crassipes* a nuisance with increasing macrophyte growth between different activities (Figure 5.6). For *Ludwigia* in Lake Grand-Lieu, activity type had no significant effect on the level of perceived nuisance.

5.3.1.2 Identifying best management alternatives for different user groups

To explore and identify the best management alternatives of macrophyte mass development for different user groups, a Bayesian network-based management decision support tool developed by Thiemer et al. (2021) was adapted. In the following two examples, the BN is adjusted to a hypothetical freshwater river that has high nutrient loadings and experiences mass development of the emergent species *S. sagittifolia*, by setting the probabilities to 100% of the states for the respective nodes (*macrophyte species, macrophyte growth* and *nutrient loading*) (Figure 5.7A). If we assume that the users of this ecosystem only consist of residents (*respondent type* set to 100% residents), the probability for a respondent to perceive high growth of *S. sagittifolia* a nuisance will then be 78% and the BN then suggests that the best management option would be full removal (probability for this option was 47%) (Figure 5.7A). By only changing the respondent type from resident to visitor, this probability of perceived nuisance decreases to 55% and the suggested management option would now be no removal (Figure 5.7B). The impact of the two different removal alternatives on the probability of high phytoplankton concentrations are considerable, where choosing full removal over no removal would result in an increased probability of algal blooms from 25% to 63%.

Assuming the same conditions as in the previous example, a goal for managers could be to manage the mass development for specific user groups, for instance anglers, boaters, swimmers or people appreciating biodiversity. By setting the activity to boating, the perception of nuisance and management alternative suggested is full removal (probability for this option was 48%), whereas changing the activity to appreciation of biodiversity, no removal is suggested (probability for this option was 40%).

5.4 DISCUSSION

The results supported the hypothesis that an increasing extent of macrophyte growth resulted in a higher probability of perceived nuisance, but differences occurred among the investigated macrophyte species and/or sites. As expected, nuisance thresholds were influenced by respondent activities and varied between respondent type with residents perceiving macrophytes a nuisance at lower levels than visitors. Contrary to the expectation, respondents with a higher ecological mindedness did not consider macrophyte growth less of a nuisance. We show that integrating this knowledge on user perceptions into a Bayesian network-based decision support tool can optimise the management of macrophyte mass developments.

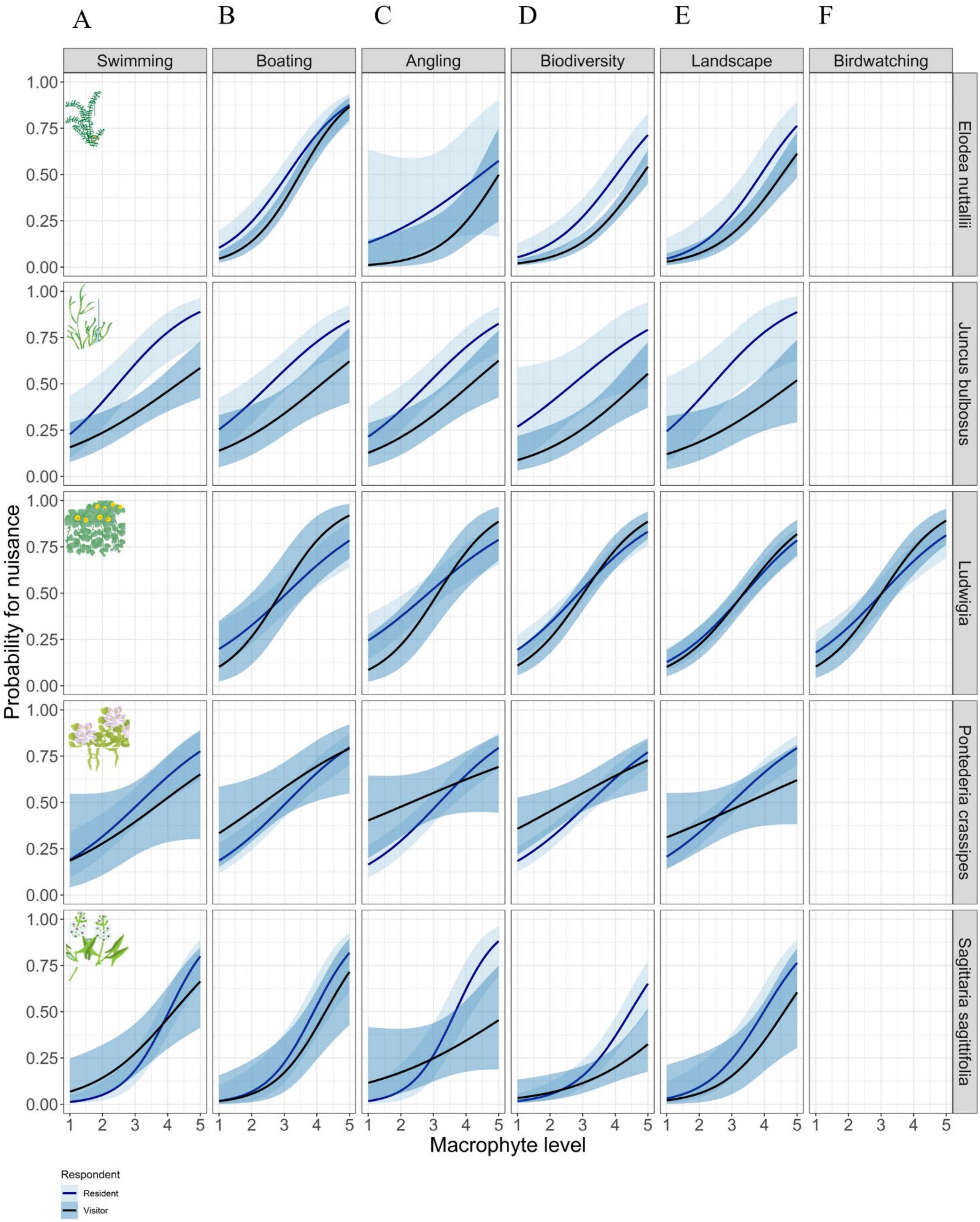

Figure 5.6: Probability of perceiving macrophytes as a nuisance with increasing macrophyte growth level, between macrophyte species and respondents for six activities (A) Swimming, (B) Boating, (C) Angling, (D) Appreciation of biodiversity, (E) Appreciation of landscape, (F) Birdwatching. Bands are confidence intervals (0.95). Note that not all activities were present in all case studies.

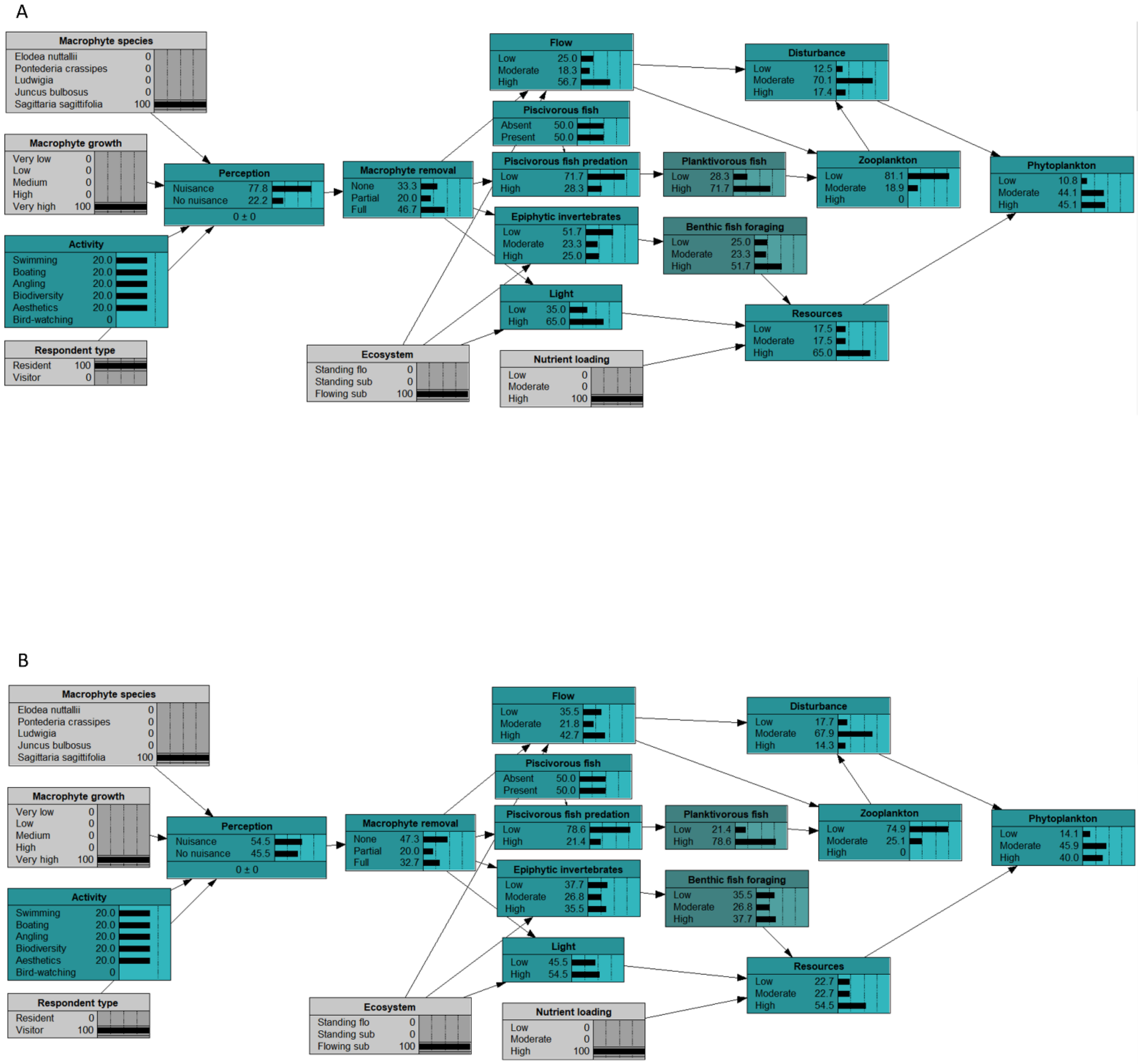

Figure 5.7: BNs of probability of management alternatives for a riverine system with high nutrient loading and very high *S. sagittifolia* growth A) Probabilities for respondent type is set to resident B) Probabilities for respondent type is set to visitors. Grey boxes indicate nodes that have been specified.

5.4.1 Identifying drivers for perceiving macrophyte growth as nuisance

The probability of perceiving macrophyte growth a nuisance was strongly related to macrophyte growth level. Interestingly, the median perceived nuisance level differed clearly among species (*J. bulbosus*: 3.6 ± 0.1, *E. nuttallii*: 4.1 (± 0.1 SD), *P. crassipes:* 3.2 (± 0.1 SD), *Ludwigia* spp.: 3.1 (±0.1 SD) and *S. sagittifolia*: 4.3 (± 0.1 SD), but we cannot disentangle the relative importance of plant species and local context due to our study design. Visitors were up to 23% less likely to consider macrophyte growth a nuisance than residents and this difference was significant for *E. nuttallii, J. bulbosus* and *S. sagittifolia*. In general, visitors often pay shorter visits to the area and may not necessarily know the local problems with macrophytes and may therefore not find the macrophyte growth a particular problem. The latter is supported by the higher proportion of visitors answering: "I don't know" to the question on which macrophyte levels they considered as nuisance growth compared to residents (visitors: 2-37%, residents:1-8%, Figure 3). Perception of *Ludwigia* spp. *w*as not different among visitors and residents. It was also expected that a high environmental-mindedness among respondents (high NEP-scores) would affect the perception and include acceptance of denser macrophyte beds. However, the NEP-score had no significant effect at all. The mean NEP-scores were similar across the five sites, ranging from 3.4-3.8, where Norwegian respondents scored comparatively low and Germans high. Correspondingly, NEP-scores reported from Norway ranged between 3.5 (Immerzeel et al., 2022) and 3.8 (Bjerke et al., 2006) and for Germany between 4.1 and 4.2 (Kaiser et al., 2005; Schultz et al., 2005). Overall, the currently observed NEP-scores fall within the expected range (3.8 ± 0.3 SD) from a meta-analysis by Hawcroft and Milfont (2010). This suggests that respondents in our five case study sites generally place an average to high value on nature and show concern about the negative impacts that human activities can have on the environment.

5.4.2 Linking nuisance perception to recreation activity type

The probability of perceived nuisance was expected to be different for each activity as well as for each case study site with different macrophyte species. In concordance with expectations, we found significant differences between activities within each case study site, but the differences were small. More interestingly, differences in perceived nuisance in relation to activity were found between macrophyte species, which indicates that perception of nuisance may not only depend on activity, but also on macrophyte species, local context and personal characteristics of the respondents. For swimmers, macrophytes are often considered a nuisance, for example when shoots entangle arms and legs (Verhofstad and Bakker, 2019), which could be a more profound problem in systems with submerged than with free-floating plants. We found that submerged *J. bulbosus* had the highest probability of being considered a nuisance at low plant densities (level 1, probability for nuisance = 25%), compared to *P. crassipes* and *S. sagittifolia* that respectively had 19% and 8% probability for nuisance at these low densities. *S. sagittifolia* was considered a nuisance at higher levels (>3), which could be a result of differences in expectations for the presence of macrophytes in this river. It is likely that respondents from lowland Germany are more used to the presence of macrophytes in rivers compared to, e.g. upland Norway, where macrophytes are generally less abundant in rivers (Haslam and Wolseley, 1987).

For recreational boaters, macrophytes are considered a nuisance when propellers get entangled (Verhofstad and Bakker, 2019) or when floating mats directly block navigation, as reported for e.g. *P. crassipes* (Habib and Yousuf, 2014; Villamagna and Murphy, 2010). It was therefore not surprising that *P. crassipes* had the highest probability of becoming a nuisance for boating activity at low macrophyte growth levels (level 1), followed by the submerged macrophytes *J. bulbosus, Ludwigia* spp. and *E. nuttallii.* Furthermore, high macrophyte growth is likely to increase the risk of rods and lines getting entangled in the vegetation, causing loss of catch and gear for recreational anglers (Verhofstad and Bakker, 2019). For anglers, growth of *P. crassipes* and *J. bulbosus* were more likely to be perceived a nuisance at low growth levels compared to *E. nuttallii* and *S. sagittifolia*. This difference cannot be explained by plant life-form and is more likely to be a result of local conditions such as difference in type of angling (deep water, shallow water, active or passive angling). Finally, appreciation of landscape and appreciation of biodiversity have to our knowledge never been considered as aspects of recreation that can drive the perception of macrophytes. *S. sagittifolia* and *E. nuttallii* were less likely to be perceived a nuisance for people's appreciation of biodiversity than the other three taxa – in their context.

5.4.3 Management implications

These results show that from a management perspective it is highly relevant to know at which level macrophytes actually are perceived as a nuisance. Macrophyte removal is rather costly (Hilt et al., 2006) and at the same time, water managers also need to secure other desired ecosystem services, such as a recreation, good water quality or a healthy fish stock. These three objectives are central for the management of freshwater ecosystems with macrophyte mass developments. The BNs developed here integrate people's perception of macrophytes with the consequences of removal and showed that management for residents may be different than management for visitors, because the latter did not mind the macrophytes as much as the former (Figure 5.7A-B). Importantly, the estimated 'optimal' management for people appreciating biodiversity in systems with macrophyte mass development was not different from that for anglers or boaters, since no differences among these categories were observed (Figure 5.6). Overall, the current BN tool can be adjusted with little effort to local conditions, because of the character of a Bayesian network. It is important to emphasise that the probabilities in the BN module dealing with the consequences (Figure 5.2) by now are based on expert knowledge. Thus, for implementation on real-word cases the states of the nodes and the conditional probabilities will have to be derived for ecosystems of interest (Thiemer et al., 2021). Finally, water managers are encouraged to consider using the developed management decision support tool and to include it in conversations with stakeholders in an early phase, i.e. when developing potential management alternatives that will balance people's perception of macrophyte growth and consequences of removal for the ecosystem.

CHAPTER 6: EFFECTS OF MANAGING NUISANCE AQUATIC PLANTS ON A SUITE OF ECOSYSTEM SERVICES

For the reader

Ås, November 14, 2022

This deliverable in its current form is a working document. Data presentation and analysis is completed to a large extent, and the introduction and methods section are also complete though yet in draft form. The whole manuscript and notably the discussion will benefit from a revision by the co-authors during the coming weeks. As soon as the draft has been circulated and reviewed satisfactorily, we will submit it to an appropriate journal.

Jan Vermaat

6.1 INTRODUCTION

Due to various underlying causes, native as well as introduced aquatic macrophytes can develop very dense stands that are experienced as nuisance and obstruct different uses of water bodies in their landscapes. This may range from recreative swimming, angling and boating (Verhofstad and Bakker, 2019), having access to schools or markets (Honla et al., 2019a, b) to flooding of adjacent land (Vereecken et al., 2006, Boerema et al., 2014), clogging of a hydropower plant intake (Dugdale et al., 2013), irrigation (Armellina et al., 1996) or commercial transport (Güereña et al., 2015).

Experienced nuisance has led to a range of control and removal measures including the use of herbicides, the release of herbivorous grass-carp or host-specific insects, sediment coverage with plastic and mechanical harvesting, which is currently the main approach worldwide (Pieterse and Murphy, 1990, Hussner et al., 2017, Hill and Coetzee, 2017, Thiemer et al., 2021). However, aquatic vegetation also provides important ecological functions (Carpenter and Lodge, 1986, Kuiper et al., 2017), which may finally affect ecosystem services that are beneficial to society (Boersema et al., 2014, Janssen et al., 2021). Thus, radical removal of aquatic vegetation may have unforeseen negative consequences through a ramified network of ecosystem relations of which the strength is not necessarily generalizable (Carpenter and Lodge, 1986, Rasmussen et al., 2021).

Experienced nuisance is a subjective perception (e.g. Gifford et al., 2011), which may not be homogeneous among different user groups or remain static with time. Thus, aquatic plant nuisance perception may be highly context-specific, depending amongst others on the predominant use of a water body (Verhofstad and Bakker, 2019), and on cultural aspects. The importance of context for both the ecosystem under scrutiny and for the perception of nuisance among residents and visitors justifies a comparative approach of specific case studies that share perceived nuisance but can otherwise differ in many ways.

This study attempted to map the most important ecological functions (or intermediate services) of aquatic vegetation onto final services that are of direct benefit to humans ('final' sensu Boyd and Banshaf, 2007), from five very different case studies where mass development of aquatic plants is considered a nuisance. The Mononen cascade framework was systematically used (Mononen et al., 2015, Vermaat et al., 2020, 2021, Immerzeel et al., 2021), which allows for a standardized comparison among cases and management measures using monetary value estimates. Whilst monetary value estimates were used in the comparative analysis, this was not intend to imply that these are directly transferable into markets. Instead, this valuation step was seen as comparable to a simplified weighing as in multi-criteria analysis (cf Wittmer et al., 2006) but also experience it as a tangible measure in communication with policy makers and the public at large.

The study objective was to assess whether different management regimes would affect the relative importance of different ecosystem services and their summed total economic value estimate (TEV). Aware of the potential predominance of context-specificity that may prevent any generalizations, the study hypothesized that moderate weed removal would lead to maximum biodiversity, aesthetic perception and sum and diversity of all quantified ecosystem services. This is in line with the assertion made by Hilt et al. (2017) or Janssen et al. (2021) that a low to moderate abundance of macrophytes would provide an optimal balance among different services.

6.2 MATERIALS AND METHODS

6.2.1 Study sites

The five study sites were selected based on reported major aquatic weed problems. Rivers and lakes that contrast in nuisance species and have different predominant types of use and geographic setting were included. Thus, the sites are very different, but the analytical framework is the same. Recreation is common to all sites, with the exception of the French Lac Grand-Lieu, where the lake itself is a strict nature reserve. A marginal zone of this lake is in use for recreation and agriculture and on the lake a few professional fishermen have access (Table 6.1; see also Thiemer et al., 2022).

6.2.2 Modelled common management regimes

For the sake of comparability, three common management regimes were used in the assessments. In recognition of the local situation, covering a wide extent whilst remaining not too far from economic and realistic feasibility. The following three regimes were chosen: 'do-nothing', 'current' and 'maximum feasible removal'. For each case, a mean growing season vegetation cover that would characterize these three regimes was deduced (Table 6.2).

Table 6.1: Description of the study sites (adopted from Thiemer, 2022).

Site (country), coordinates (lat/long) *	Area, annual mean discharge	Important current forms of use	Nutrient status	Nuisance species	Mean plant biomass (g DW m^{-2})
River Otra at Rysstad (Norway) 59.088/-7.550	69 m^3 s^{-1} upstream of the study reach 11 km length and 210 ha	Hydropower, recreation	Oligotrophic	submerged *Juncus bulbosus,* canopy often reaching the water surface	148 ± 35
River Spree from Grosse Tränke to Lake Dämeritz (Germany) 52.430/-13.678	14 m^3 s^{-1} for a reach of 34 km length and an area including floodplain of 2050 ha	Recreation, agriculture in the floodplain	eutrophic	Submerged and emergent *Sagittaria sagittifolia*	335 ± 61
Lake Kemnade (Germany) 51.416/-7.260	125 ha, created in the valley of the river Ruhr	Recreation, hydropower, drinking water, flood regulation	Eutrophic	Submerged *Elodea nutallii,* canopy reaching the water surface	421 ± 180
Lake Grand Lieu (France) 47.133/-1.674	Seasonal variation with summer drawdown, 3500 – 6300 ha; summer level open water 2700 ha and wet pastures 2400 ha	Strict nature reserve, some fisheries; recreation and agriculture along its banks	Eutrophic	Emergent and amphibious *Ludwigia grandiflora* and *L. peploides* (mixture of two species difficult to separate for the non-expert)	183 ± 85
Lake Hartbeespoort Dam (Republic of South Africa) -25.749/ -27.833	Reservoir, 1850 ha	Irrigation, drinking water, recreation	hypertrophic	Free-floating *Pontederia crassipes*	972 ± 137

*negative latitudes are S of the equator, negative longitudes are E of Greenwich.

Table 6.2: Estimated percentage mean vegetation cover at (or near) the water surface for the three management regimes and five cases.

Site	Do nothing	Current	Maximum removal	Source of information
River Otra	65	64	35	MADMACS fieldwork*
River Spree	60	40	10	MADMACS fieldwork
Lake Kemnade	90	44	0	Podraza et al. (2008) and MADMACS fieldwork
Lake Grand Lieu (In water + on shore)**	4+6	3+5	0+0	SNPN (2017), MADMACS fieldwork
Lake Hartbeespoort Dam	50	40	10	Mitchell and Crawford (2016), MADMACS fieldwork

*Susi Schneider compiled field work cover data and estimated plausible cover values for the three regimes in all the five cases in an unpublished report.

** In Grand Lieu, the *Ludwigia* species expanded along the shoreline and cover parts of both nearshore water as well as wet pastures.

6.2.3 Ecosystem services framework

The Mononen cascade was deployed to relate nuisance vegetation cover to a range of final services via the effect on a network of ecosystem functions (or intermediate services) that would have an effect on these final services. For this purpose, we first compiled a matrix of potential functions and final services and deduced their relations based on literature. For each case, we selected the functions and final services from the matrix that would be relevant and then compiled information quantifying both functions and services, as exemplified in Figure 6.1 and Table 6.3 for the services included. Table 6.3 stipulates our approach to estimate each service and gives the sources of information used. Compilation was done in a spreadsheet, and the values used were quality checked by all co-authors including those that had case-study-specific experience. Each spreadsheet contains a page with an overview flow diagram that allows plant cover to be varied and then displays the consequent biophysical and monetary value estimates of each final service, and includes a summation of these into Total Economic Value (TEV).

Data from questionnaire surveys carried out for the MadMacs project at each site were used to estimate values of cultural services (cf Immerzeel et al., 2021, 2022). These surveys are analysed and described in more detail in Thiemer et al. (in press). The question where (i) respondents were asked to indicate at what level out of five they perceive the plants to be a nuisance, the question whether they consider themselves resident or non-resident, (ii) the question where respondents were asked to distribute 100 points over several services to indicate their priorities (bathing, boating, angling, awareness and appreciation of biodiversity conservation, appreciation of the scenic landscape), and (iii) the question inquiring after the distance travelled; were used.

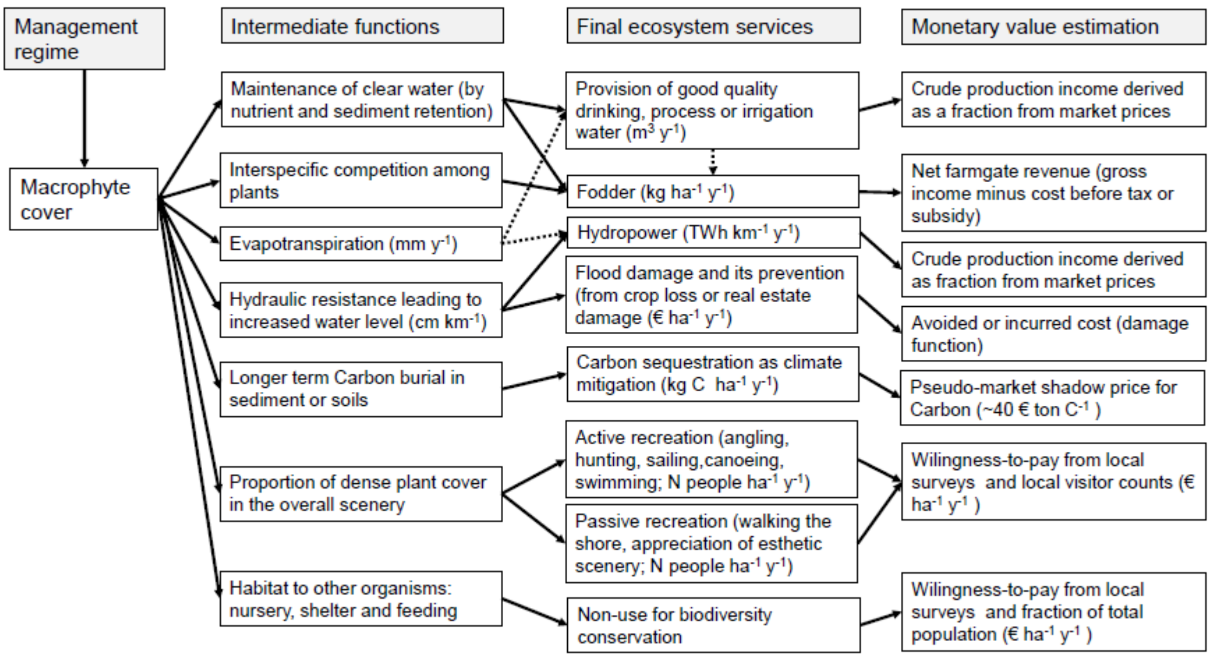

Figure 6.1: Flow scheme relating nuisance plant management regimes via macrophyte cover and intermediate ecosystem functions to final ecosystem services in biophysical terms and monetary values. Only functions and services depicted that were common to several cases. For each case we started from a larger number of functions and services in an extensive spreadsheet table. Broken arrows indicate that the relation is potentially important in some of the cases (see also Table 6.3).

Table 6.3: Final ecosystem services quantified in the five case studies including their links to ecosystem functions. The CICES code is conform Haines-Young and Potschin (2017), a benchmark classification of ecosystem services.

Final service (CICES code)	Relation to function/intermediate service	Relevant in case*	Quantification in biophysical terms	Monetary valuation approach	Source of information
Fodder (1.1.1.1)	Flooding of floodplain, competition by invasive weeds	S, G	Reduction in yield or area accessible for cattle grazing by flooding or competition	Net farmgate revenue	Farm yield statistics: Landesamt, etc. (2020) and Agreste (2019).
Compost (~1.1.1.1)	Harvested water hyacinth	H	Biomass collected and processed into compost for gardening	Crude net farmgate revenue as 10% of reported consumer price	About 2% of the standing stock of water hyacinth reportedly has been harvested as part of the Metsi a Me project (Mitchell and Crawford (2016), see also the compost company website: www.hyamatlaorganics.co.za
Professional fisheries (~1.1.3.1)	Increased plant growth may impede boating and gear.	G	Change in quantity of fish landed	Crude revenue estimate as 50% of consumer price	Baldo (2020): no measurable effect on fish yield in Lake Grand-Lieu.
Drinking water (4.2.1.1)	Maintenance of clear water (CICES 2.2.5.1) by nutrient or suspended sediment retention	O, S, K, H	Effect on drinking water production	Crude estimate of production costs as 50% of consumer price	Local drinking water companies; no effect of more or less nuisance plants estimated for O (extraction from river occurs but negligible), G, H, S (bank infiltration is only 9% of annual river flow), K (flow too high)
Irrigation water for crops (4.2.1.2)	Maintenance of clear water (CICES 2.2.5.1) by nutrient or suspended sediment retention; possibly evapotranspiration losses	H	Effect on total volume of irrigation water available of sufficient quality: more or less water hyacinth compared to current will lead to less or more transpiration, corrected for differences in evaporation from the free water surface	Estimate of irrigation water price: 0.26 rand or 0.02 € m^{-3}	Fraser et al. (2016)

Final service (CICES code)	Relation to function/intermediate service	Relevant in case*	Quantification in biophysical terms	Monetary valuation approach	Source of information
Hydropower (4.2.1.3)	Sufficient (geomorphological) gradient	O, H	O: Dislodged and decaying plant material clogs the downstream water intake at Hekni, this material is regularly removed	O: the removal occurs at negligible cost, the detritus is deposed of on-site	H: no longer used for hydropower (Ashton et al., 1985) O: personal observation
Flood prevention (2.2.1.3)	Hydraulic resistance of dense beds increases water level upstream	S, G	Increased water level affects groundwater level in the floodplains; dense nuisance plants may increase ponding and flood risk; affects crop yield or domestic infrastructure	Net farmgate revenue; domestic infrastructure via a damage function	As in Vermaat et al. (2021), based on De Moel and Aerts (2011); for the Spree also Lewandowski et al. (2009) and Köhler (unpublished).
Erosion prevention (2.2.1.1)	Dense plant beds may protect the physical shore from potentially eroding wave exposure	S	Length of shoreline retreating, possibly leading to land loss	Investment in bank protection, vale of lost land	Has been suggested for the Spree by Köhler (pers. comm.) but has not been quantified.
Carbon sequestration for greenhouse gas mitigation (2.2.6.1)	Part of the plant biomass produced is buried in the sediment and will be subject to slow decay and longer-term storage	All	Decaying biomass stored in the sediment	From the shadow market a carbon price of 40 € ton C-1 is taken.	This estimate is the lower quartile of the range observed in the European Emission Trading System (20-100) from 2020-2022, and it is in range with the estimates of the global social cost of carbon for 5 SSP scenarios in Tol (2019)

Final service (CICES code)	Relation to function/intermediate service	Relevant in case*	Quantification in biophysical terms	Monetary valuation approach	Source of information
Active Recreation (boating, angling, swimming; 3.1.1)	Dense plant beds impede activities	All	Optimum curve of perceived impediment versus plant cover	Appreciation combined with willingness to pay from survey and a proportion of the population – case-specific	Derived from survey data in Thiemer et al. (in revision): mean travel distance for residents and non-residents multiplied by a conservative low-end travel cost from Juutinen et al. (2022) of 0.05 € km-1
	Maintenance of clear water (CICES 2.2.5.1) by nutrient or suspended sediment retention;	O, S	Effect on recreative appreciation	Water requires sufficient clarity for bathing; incorporated into recreative appreciation	Derived from survey data in Thiemer et al. (in revision)
Passive (beach) recreation, appreciation of scenery (3.1.2)		All	Optimum curve of perceived impediment versus plant cover	Appreciation combined with willingness to pay from survey and a proportion of the population – case-specific	Derived from survey data in Thiemer et al. (in revision)
Biodiversity non-use (3.2)		All	Appreciation declines with increasing nuisance plant cover	Appreciation combined with willingness to pay for non-use from survey and a proportion of the population – case- specific	Derived from survey data in Thiemer et al. (in revision) and Garcia et al. (2011) for France.

*O=Otra, S=Spree, K=Kemnader See, G= Grand Lieu, H = Hartbeespoort Dam

The number of respondents varied among sites, and so did their travel distance (Table 6.4); note that not all respondents filled out all questions completely so that totals may not fully correspond among the different questions.

Table 6.4: Number of resident and non-resident respondents that completed the survey for the questions analysed here. We also include an estimate of travel distance (mean ± standard error).

Site	n residents	n visitors	n total	Travel distance residents	Travel distance visitors
River Otra	62	83	145	6.9±3.5	176.0±19.3
River Spree	134	77	211	4.0±1.8	44.1±10.1
Lake Kemnade	149	174	323	8.4±0.5	23.8±2.1
Lake Grand Lieu	177	129	306	5.5±0.8	75.8±7.6
Lake Hartbeespoort Dam	210	65	275	9.4±1.2	72.0±21.0

6.3 RESULTS

In three out of the five cases, major changes in aquatic plant cover had little or no effect on TEV the estimated summed value of all quantified final ecosystem services (Figure 6.2), and for both the Spree and the Otra this involved a considerable span in cover, hence also in effort of weed removal. The Kemnader See and Hartbeespoort Dam showed different patterns. In the former, the major increase in cover in the 'do-nothing' regime did have an effect mainly on the aesthetic appreciation (Figure 6.3) of the place by the more passive recreation on the banks of the lake, like walking and pick-nicking. In the latter, however both the increase and the reduction in water hyacinth cover affected TEV, and this was mainly due to boating and angling (Figure 6.3). None of the five cases show an optimum in TEV at intermediate plant cover, hence our tentative hypothesis is not supported.

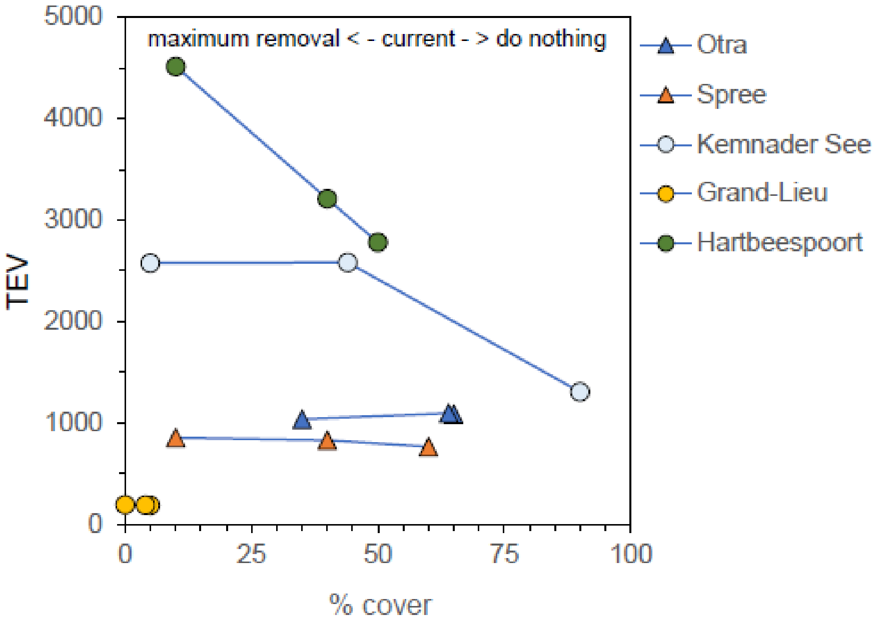

Figure 6.2: Effect of management regime (do-nothing, current, maximum removal) via aquatic plant cover on the sum of ecosystem services provided (TEV, € ha^{-1} y^{-1}) in the five study sites.

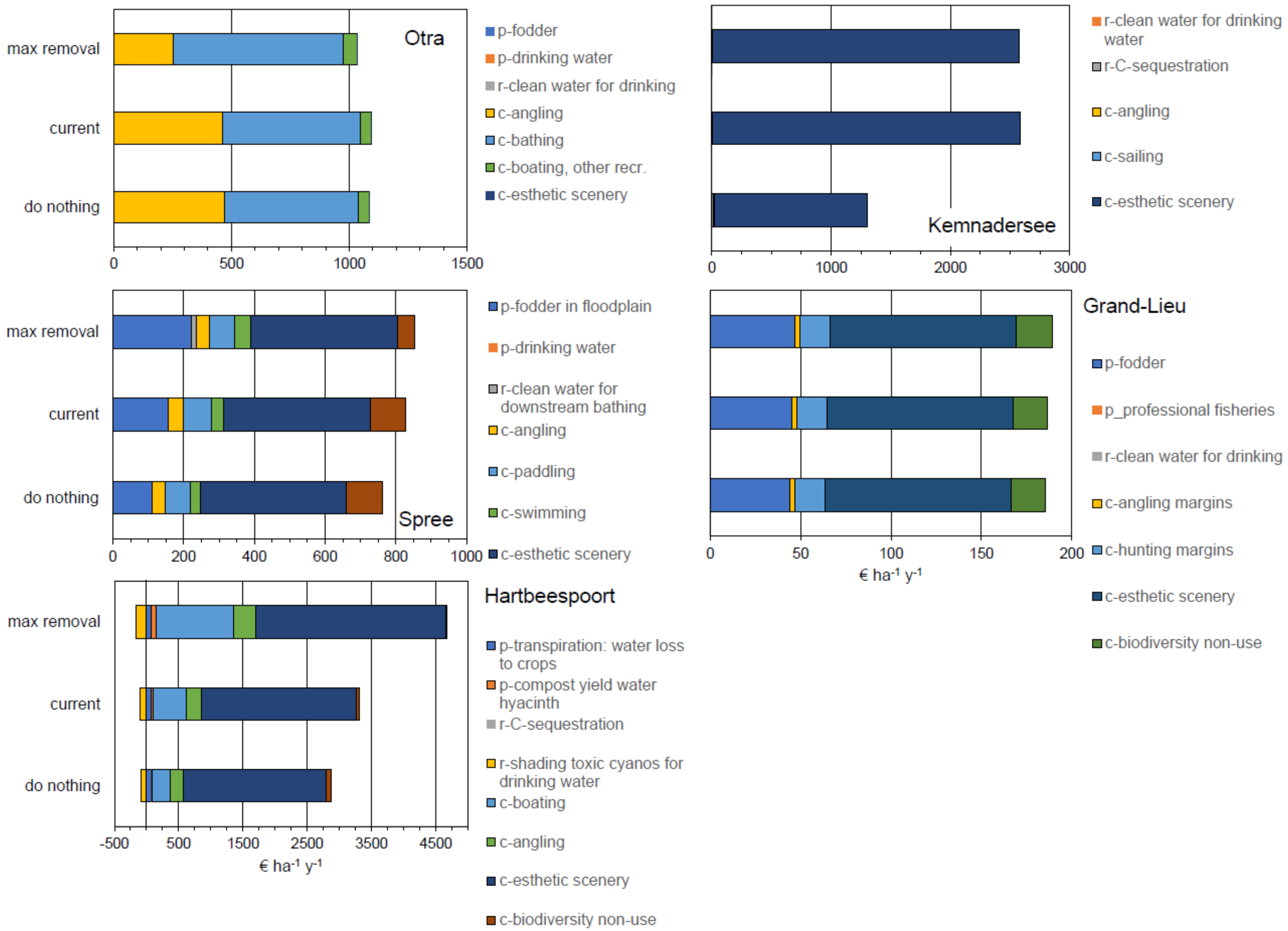

Figure 6.3: Effect of management regime (do-nothing, current, maximum removal) via aquatic plant cover on the importance of different services to the summed TEV. The different services follow the same legend, but some services are absent or negligible in some study sites. The suffix ‘p-‘, ‘r-‘ and ‘c-‘, respectively, denote that this is a provisioning, regulating or cultural service.

The River Spree had the most diverse portfolio of uses. Despite its location near Berlin, the total number of residents and visitors engaged in recreation was much lower than in the other German site Lake Kemnade likely due to the availability of many more alternatives around Berlin than in the densely populated Ruhrgebiet. The strict nature reserve of Grand-Lieu clearly had the lowest Total Economic Value. This is very likely due to the limited access, although the marginal zone attracts recreation, also from nearby Nantes. Likely the nearby Atlantic coast also offers attractive alternatives.

Whereas different forms of recreation (i.e. cultural services) generally dominated the estimated total value in all five cases, the relative distribution contrasted strongly among them (Figure 6.3). Only in the Spree and Lake Grand Lieu, the provisioning service 'fodder' to grazing cattle in the floodplain or wet meadows contributed substantially to the total (respectively 19% and 24% under the 'current' regime. The Spree had the most diverse palette of services provided. In Hartbeespoort Dam reduced water hyacinth cover would lead to an increased incidence of toxic cyanobacteria. It was estimated that this would increase the cost of drinking water production, hence can be interpreted as a disservice. However, this was completely overshadowed by the increased benefit of particularly increased boating and angling. Interestingly, the analysis captured very few trade-offs among different services. The only apparent one is a trade-off in the Spree between the provision of fodder (higher at low water plant density and more rapid drainage with lower water levels) versus the biodiversity value due to increased survival probability of red-listed wetland plant species (higher with high plant density and raising river water levels with increased impoundment; Figure 6.3).

Preference distributions among categories respondents (Figure 6.4) have been used to estimate when cover in our three regimes would be expected to create a perceived nuisance – and this was used as a modifying knowledge rule to estimate the monetary value of the different forms of recreation (compare to Table 6.3 and Figure 6.3). These preference patterns in themselves also differed substantially among sites and types of respondents (Figure 6.4). Firstly, residents perceived a nuisance at lower levels than current and then visitors in the Otra, the Spree and likely Hartbeespoort Dam ($p<0.10$ only). Secondly, only in the Otra a substantially higher proportion of the visitors found the plants no problem or concluded that 'they did not know', and interestingly, significantly more residents in Grand Lieu found that these dense stands of invasive *Ludwigia* are no problem. Here it is those that appreciate the scenery who also find 'the weeds no problem', whereas as those interested in biodiversity are already concerned at a low cover (Figure 6.4). Only in the Otra and Hartbeespoort Dam, few recreative users answered that weeds are no problem', whereas in the two German cases a large proportion of those that appreciated biodiversity most also find weeds no problem.

6.4 DISCUSSION

The study hypothesis was not supported – on the contrary, in three out of the five cases any effect of more or less weed cover on our estimate of total economic value was absent. Only in one case, Hartbeespoort Dam with a high cover of water hyacinth, we found a clearly positive effect of increased removal effort. This should serve as a cautionary message to water managers: particular user groups may be vocal in demanding more effort, but the effect on the total societal benefit may be questionable, and a careful consideration of the importance of different user categories is clearly warranted. Then, over and above any context-specificity and irrespective of management regime, an overruling importance of recreation was observed in all five cases, be it in the water and more active or on the banks and less active. Such an importance of recreation relative to for example provisioning services, such as agricultural food production or silvicultural timber production was also found by Immerzeel et al. (2021). Boerema et al. (2014) valued ecosystem services provided by a Belgian lowland stream network that is subject to regular aquatic plant removal. These authors, however, did not include recreation in their assessment. They found that the annual cost of weed removal was only narrowly compensated by the benefits and this is mainly due to flood prevention of agricultural land. Boerema et al. (2014) concluded that if only a few ecosystem services would be included in the cost-benefit assessment before deciding on weed removal, the benefits of removal would already be negative.

The predominance of recreation in the monetary value estimates makes this approach necessarily sensitive to errors in the number of people that engage in the different forms of recreation, and to the way we estimate an individual willingness-to-pay. The former was indeed particularly uncertain for Hartbeespoort Dam, where in the absence of reported data we assumed the number of visitors to be a simple multiple of 10 times the number of residents. Given the considerable availability of facilities around the Dam this is likely a rather conservative factor. Reducing this factor 10 substantially would not have altered the overall pattern for this site. For the other sites public statistics were available or visitor numbers could be estimated from parking lot counts (Kemnader See). For the individual willingness-to-pay, a low-end travel cost was used, assuming private car or public transport (the latter for visitors of the Müggelsee, a lake in Berlin popular for bathing and immediately downstream of our section of the Spree, Table 6.3).

An important finding from the surveys is that different forms of recreation predominate in different sites. In the River Otra (angling and boating) and Hartbeespoort dam (angling, boating), active recreation on the water contributed importantly to overall societal benefit. In the River Spree, Lake Kemnade and Lake Grand-Lieu this was rather a more passive form of recreation on the banks (weekend trips, walks, picknicks). Since visitors engaging in these different forms of recreation differ greatly in their perception of nuisance (Figure 6.4, left panels).

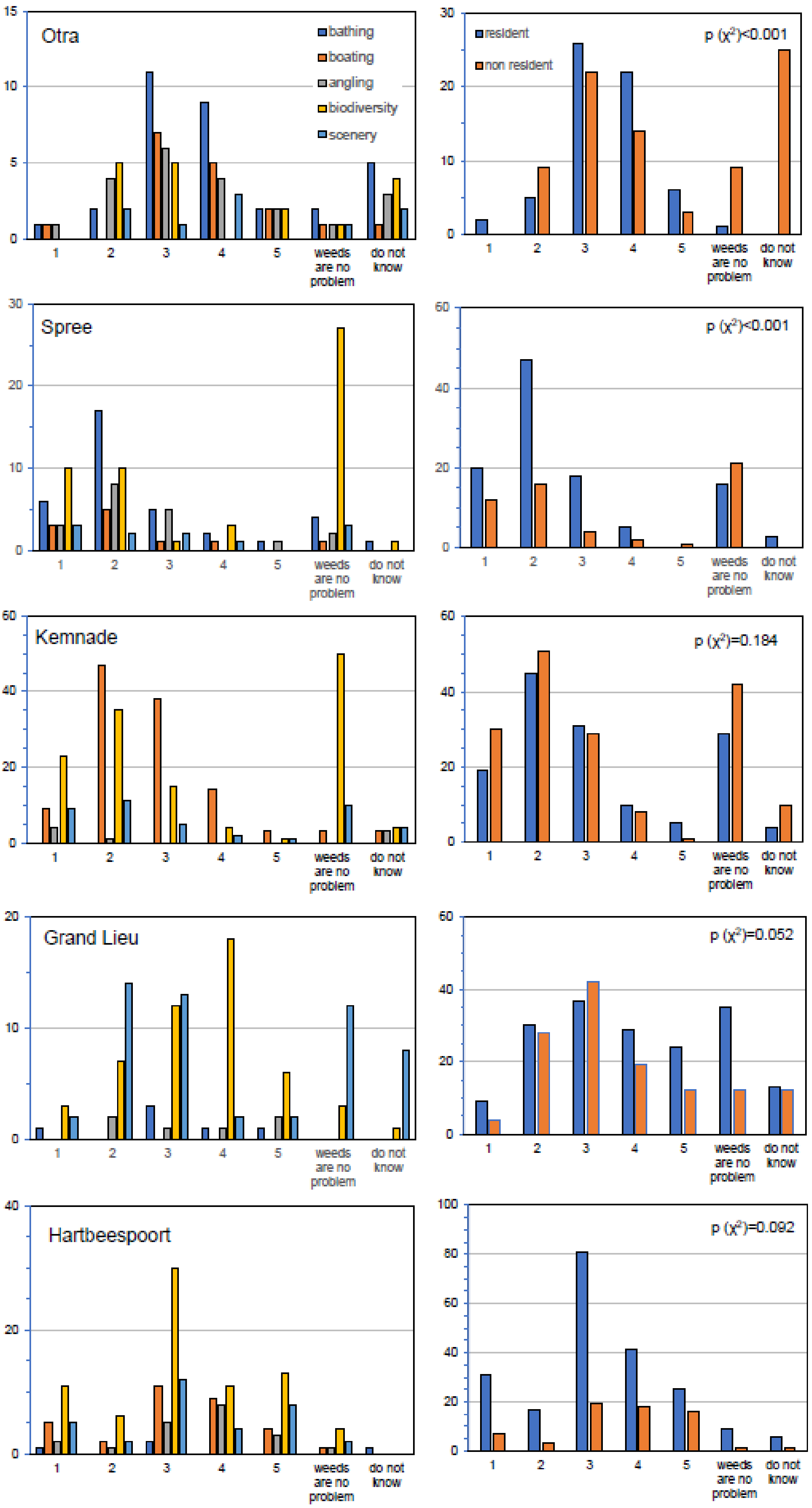
Otra
Spree
Kemnade
Grand Lieu
Hartbeespoort
bathing
boating
angling
biodiversity
scenery
resident
non resident
p (χ²)<0.001
p (χ²)<0.001
p (χ²)=0.184
p (χ²)=0.052
p (χ²)=0.092
1
2
3
4
5
weeds are no problem
do not know

Figure 6.4 (on previous page)**:** Left: Aquatic plant density at which different groups of survey respondents experience nuisance. A respondent was selected to belong to a group when she/he allocated 50 or more of the available 100 points to this final service. Right: the same, but for the two categories resident and non-resident. Here a X^2 test was done to assess whether the distribution differed between residents and visitors, and the resulting level of significance is indicated in the top right corner. Respondents could select 5 different levels of plant cover, with level 1 being highest (100% of the water surface covered) and 5 lowest (generally 0%). Raw data were processed envisaging a respondent moving up from low to high cover and deciding where nuisance is experienced. Current vegetation cover corresponded to level 2 in all cases except Hartbeespoort Dam, where it was level 3. Note that the length of the vertical axis differs among graphs.

CHAPTER 7: KEY MESSAGES FROM THE MADMACS PROJECT

The major findings and conclusions of the MadMacs project as a set of nine key messages are presented in this chapter.

7.1. Mass developments of macrophytes often occur in ecosystems which (unintentionally) were turned into a «perfect habitat» for aquatic plants

Macrophytes need resources (nutrients, light) for growth, while disturbances (e.g. floods, grazing) limit macrophyte development. Therefore, nutrient enrichment generally enhances the growth of macrophytes, while reduced disturbance, e.g. caused by watercourse regulation, minimises the loss of plant biomass, thereby enabling the build-up of large plant biomasses over time. The “perfect habitat” for aquatic plants provides enough light for plant growth, has sufficient nutrients in water and/or sediment, and presents little mechanical disturbance. In such ecosystems, both native and non-native aquatic plants can form dense stands.

Figure 7.1: The “perfect habitat” for submerged aquatic plants is shallow, provides enough light and nutrients for plant growth, and experiences few mechanical disturbances. In such habitats, dense biomasses of aquatic plants are common (top left: *Juncus bulbosus* and *Myriophyllum alterniflorum* in the regulated River Mandalselva, Norway; top right: several species of native macrophytes in the regulated and moderately nutrient rich River Spree, Germany; bottom left: floating macrophytes and cyanobacteria in the nutrient rich Hartbeespoort Dam, South Africa; bottom right: submerged *Egeria densa* in the slowly flowing nutrient rich River Kouga, South Africa). Photo: S. Schneider (top left), J. Köhler (top right), J. Coetzee (bottom)

Examples from MadMacs

- **Native, submerged bulbous rush (*Juncus bulbosus)* in the River Otra (Norway)** – River regulation has created large shallow, slow-flowing areas that are permanently inundated and little disturbed by floods, droughts, or ice-scraping. These conditions enable perennial growth of submerged macrophytes despite low water nutrient concentrations. High macrophyte biomasses are accumulated over several years.
- **Native, submerged macrophytes in the River Spree (Germany)** – River regulation has created a slow-flowing river that experiences few disturbances, while nutrient concentrations are just right to support massive growth of annual macrophytes without leading to phytoplankton blooms (which could reduce submerged macrophyte growth via reduction of the light available to macrophytes).
- **Non-native, submerged Nuttall's waterweed (*Elodea nuttallii)* in Lake Kemnade (Germany)** – Regulation of the River Ruhr created a lake with large shallow areas that are little disturbed by floods or droughts. Nutrient concentrations are just right to enable massive growth of submerged macrophytes without leading to phytoplankton blooms.
- **Non-native, free-floating water hyacinth (*Pontederia crassipes)* in Hartbeespoort Dam (South Africa)** – The construction of the dam created a lake with limited flow and extremely high nutrient concentrations from urban waste. Because the water is deep and turbid, few submerged macrophytes grow, but conditions are ideal for the massive growth of free-floating macrophyte species.
- **Non-native, emergent water primrose (*Ludwigia* species) in Lake Grand Lieu (France)** – The water level of this shallow lake is managed by a sluice gate, creating large shallow areas that are inundated during winter, while the water level is low during summer. Because the water is turbid, few submerged macrophytes grow. The lake shore, however, is ideal for the massive growth of amphibious plants (which can grow in water and on moist soil), while the nutrient rich water in the center of the lake is ideal for floating-leaved and free-floating macrophytes.
- **Non-native, emergent tanner grass (*Urochloa arrecta)* in the River Guaraguaçu (Brazil)** – This tidal river is slow-flowing and a few meters deep. Nutrient concentrations are high due to poorly treated domestic effluents, particularly during the summer season. Tanner grass can tolerate changing salinity and has a high growth rate, producing a large amount of biomass in a short time, outcompeting native aquatic plants. The combination of high nutrient input, slow flow and quick development makes this site ideal for massive growth of tanner grass.

Supporting information

"Perfect habitat" conditions differ among aquatic plant species and growth forms, but they have in common that a lack of disturbances enables the build-up of massive biomasses. Free-floating plant species need high nutrient supply, tolerate turbid water and, because they float at the water surface, occur at all water depths. Emergent species need high nutrient supply from the sediment, tolerate turbid water and some flow, but need shallow areas. Submerged species only grow in water that is sufficiently clear to enable photosynthesis under water. Via a positive feedback, mass developments of submerged macrophytes enhance water clarity, thereby promoting further plant growth. Due to their need for light under water, mass development of submerged macrophyte species generally occurs in relatively shallow water, from about 0.5 to about 4 m water depth (the exact depth may vary depending on water clarity and plant species). The mass development of annual submerged macrophyte species depends on sufficient nutrient supply and sufficient access to light in spring to enable the build-up of large biomasses within one vegetation period. In contrast, perennial species can grow slowly in nutrient-poor ecosystems and may build up massive biomasses over several years, provided disturbances are low and there is enough access to light.

7.2. Reduced ecosystem disturbance can cause macrophyte mass developments even if nutrient concentrations are low

Aquatic plants generally grow slowly in ecosystems where nutrient availability is low. In freshwater ecosystems with little disturbance, however, perennial aquatic plants can build up massive biomasses over several years, despite low nutrient concentrations. Permanently inundated, shallow areas in regulated freshwater ecosystems with relatively stable discharge and water depth are therefore prone to mass developments of macrophytes, even if water nutrient concentrations are low.

Figure 7.2: River stretches downstream of the outlet of hydropower plants experience few floods, and water temperatures are relatively low in summer, while there is no ice cover in winter. In these conditions, submerged aquatic plants can stay wintergreen and build up massive biomasses over the course of several years, even though nutrient concentrations in water and sediment are low. In Norway, bulbous rush (*Juncus bulbosus*; left) is often perceived as the worst species but others, including floating pondweed (*Potamogeton natans*, right), alternate water-milfoil (*Myriophyllum alterniflorum*) and narrow-leaved bur-reed (*Sparganium angustifolium*) may also build mass developments.
Pictures: S. Schneider.

Example from MadMacs

- Regulation of the River Otra (Norway) has created large slowly flowing, permanently inundated areas that are little affected by floods, droughts or scraping of the river bottom during the spring ice-melt. This enables perennial growth of *Juncus bulbosus*, a submerged aquatic plant species, despite very low water nutrient concentrations (< 3 µg/ℓ SRP; 0.03 mg NO_3-N/ℓ). High aquatic plant biomasses are built up over several years, and there is some evidence that the aquatic plants not only survive winter as green plants, but may continue to grow throughout winter, in areas where there is no ice cover due to hydropower generation. Massive aquatic plant biomasses occur from about 0.5 to 4 m water depth, i.e. where underwater light conditions enable plant growth.

Supporting information

The results from MadMacs suggest that only perennial aquatic plant species can build mass developments in nutrient poor ecosystems, because growth of annual species is limited by low nutrient availability. The biomass that is built up during one growing season is therefore unlikely to reach “nuisance” levels in nutrient-poor ecosystems.

Many aquatic plant species may, however, stay winter-green when water temperatures are above zero, when there is enough light, and disturbance level is low. When assessing the risk of macrophyte mass developments in regulated, nutrient poor ecosystems, it is therefore important to take the potential plasticity of macrophyte life cycles into account. It is important to consider potential issues with macrophyte mass developments when planning river regulation, e.g. for hydropower generation or irrigation, even if water nutrient concentrations are low

7.3. Macrophyte removal treats the symptom rather than the cause

The underlying reasons for the mass development of aquatic plants are generally related to an increased availability of limiting resources and/or a decreased intensity of disturbances. Without targeting the underlying reasons for the massive plant growth, the available resources will likely be used by other primary producers upon macrophyte removal. This may lead to increased growth of phytoplankton, periphytic algae, or other aquatic plant species. Most often, however, the removed species will simply re-grow if environmental conditions are not addressed.

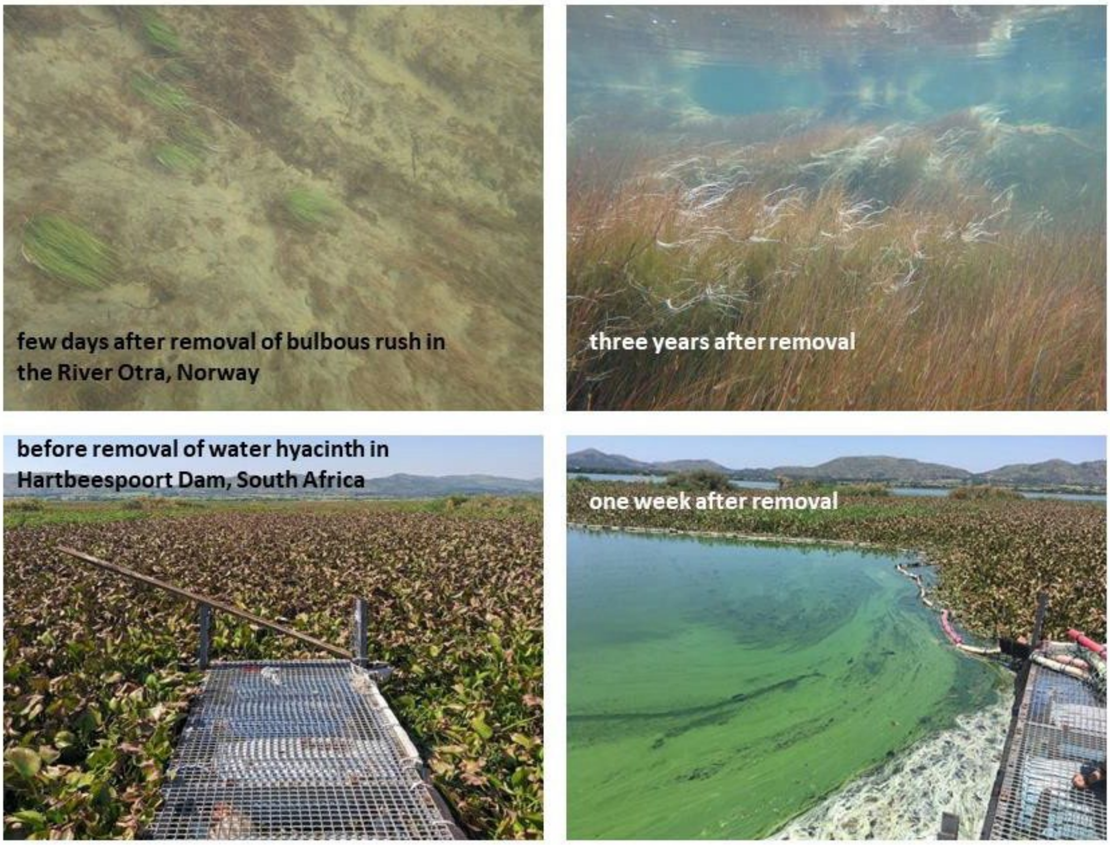

Figure 7.3: Plant cutting followed by sediment harrowing significantly reduced the biomass of bulbous rush (*Juncus bulbosus*) in the River Otra, but some plants remained (top left). Three years after the mechanical removal, the plant biomass had fully regrown (top right). In nutrient-rich ecosystems, plant removal may lead to the mass development of algae and cyanobacteria, as we observed in Hartbeespoort Dam, where dense water hyacinth (bottom left) was replaced by cyanobacteria after only a few days (bottom right). Pictures: S. Schneider (top), J. Coetzee (bottom left) and A. Petruzella (bottom right)

Examples from MadMacs

- Free-floating water hyacinth (*Pontederia crassipes*) in Hartbeespoort Dam was previously combated using herbicides. After spraying *P. crassipes* biomass, massive blooms of cyanobacteria occurred in Hartbeespoort Dam, an effect which we also observed in our mechanical macrophyte removal experiment. The cyanobacterial bloom likely has benefitted from a combination of high nutrient availability, removal of shading by free-floating aquatic plants, as well as liberation from allelopathic substances which *P. crassipes* normally releases, turbid water preventing the growth of submerged plants and periphytic algae, and high water temperatures enabling fast cyanobacterial growth.
- Upon experimental removal of submerged Nuttall's waterweed (*Elodea nuttallii)* in Lake Kemnade, we observed an increase in periphytic algal biomass. The periphytic algae likely benefitted from high nutrient concentrations and the removal of shading from tall macrophytes.
- Mass development of the non-native free-floating water hyacinth (*Pontederia crassipes)* in Hartbeespoort Dam is currently combated by biocontrol, i.e. by releasing insects that specifically target *P. crassipes* while leaving other plant species untouched. Recent observations indicate that another free-floating plant species, *Salvinia minima*, has increased in biomass, while *P. crassipes* declined. The other free-floating plant species likely benefits from high water nutrient concentrations, decreased competition with *P. crassipes* for resources and space, and the fact that the released biocontrol agents specifically target *P. crassipes*, thereby favouring competing plant species.
- 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). This indicates that if the underlying

Supporting information

When disturbance levels are low and growth conditions are good, available resources generally will be used by primary producers, leading to plant and algal growth. When mass developments of macrophytes are mechanically removed while environmental conditions remain unchanged, it is likely that either the removed species will grow back, or other primary producers will take over. Habitat conditions determine which group of primary producers is likely to dominate after the removal of macrophytes. Phytoplankton blooms typically develop quickly in lakes where water nutrient concentrations are high, the abundance of zooplankton grazers is low (for example due to a high abundance of fish feeding on zooplankton) and turbidity prevents light from reaching the lake bottom, thereby excluding the growth of benthic primary producers. 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). Shortly (few days to weeks) after macrophyte removal, algae that have fast growth may dominate. Few weeks to several years after the macrophyte removal, however, re-growth of the removed macrophyte species is likely to occur. Regrowth is likely to happen rapidly (few weeks) in nutrient rich ecosystems with warm water, and slowly (few years) in nutrient poor, cold ecosystems. Over many years, mechanical removal generally favours fast growing macrophyte species that can spread vegetatively from plant fragments. This may lead to a change in macrophyte species composition, but generally does not solve the problem of perceived macrophyte nuisance growth.

7.4. Removal of non-native macrophytes may lead to nuisance growth of other macrophytes

All macrophytes need resources for growth, while disturbances limit macrophyte development. This is true for both native and non-native species. Removal of non-native macrophyte species alone may therefore not solve the problem of perceived macrophyte nuisance growth, because other macrophyte species may take over, creating similar problems for the users of the ecosystem.

Figure 7.4: Mass development of the non-native free-floating water hyacinth (*Pontederia crassipes*) in Hartbeespoort Dam is currently combated by biocontrol, i.e. by releasing insects that specifically target *P. crassipes* while leaving other plant species untouched. Recent observations indicate that another free-floating plant species, common salvinia/water spangles (*Salvinia minima*), has increased in biomass, while P. crassipes declined. This indicates that the targeted removal of a non-native macrophyte species may not solve the problem of perceived nuisance growth, because other plant species take over, creating similar problems for the users of the ecosystem. In the pictures, *S. minima* is visible as "green carpet", while the larger plants are *P. crassipes*. On the top picture, *P. crassipes* partly has a brown colour, due to feeding damage caused by the biocontrol agents. Pictures: J. Coetzee.

Examples from MadMacs

- Areas up to about 4 m water depth in Lake Kemnade (Germany) are currently overgrown by massive amounts of the **non-native** Nuttall's waterweed (*Elodea nuttallii)*. Anecdotal information, however, reports massive growth of unknown but probably native macrophyte species in similar nearby lakes created along the River Ruhr in the beginning of the 20th century, i.e. at a time when *Elodea nuttallii* was not widespread in Germany. The plants were reported to clog the intake of hydropower plants, and hinder boating, sailing and swimming. This indicates that massive growth of both native and non-native plant species may occur in lakes along the River Ruhr when conditions are "right", i.e. when there are enough resources for plant growth and when disturbance is low. It is, therefore, likely that nuisance growth in Lake Kemnade could also be built up by **native** plant species capable of fast growth. Potential species include, e.g. Eurasian watermilfoil (*Myriophyllum spicatum)*, hornwort (*Ceratophyllum demersum)*, shining pondweed (*Potamogeton lucens)*, or sago pondweed (*Stuckenia pectinata)*. "Elimination" of non-native *Elodea nuttallii* would therefore, even if it was possible, likely not solve the problem of perceived plant nuisance growth in Lake Kemnade, because other plant species would take over, creating similar problems for the users.
- Mass development of the non-native free-floating water hyacinth (*Pontederia crassipes*) in Hartbeespoort dam is currently combated by biocontrol, i.e. by releasing insects that specifically target *P. crassipes* while leaving other plant species untouched. There are, however, first signs of other free-floating plant species taking over while *P. crassipes* is reduced. This indicates that the targeted removal of non-native plant species alone may only

Supporting information

Non-native macrophyte species may have a competitive advantage over native species, because, for example, they are less grazed upon, use the available nutrients in a more effective way, tolerate lower light conditions, or have a higher growth rate than native species. For these reasons, non-native plants may produce higher biomasses than native species with a comparable growth form and life cycle. Non-native plant species may threaten local aquatic biodiversity. There are, therefore, good reasons to combat non-native plants. In cases where the goal of the removal, however, is to remove perceived plant nuisance growth, e.g. to improve conditions for boating, swimming, or angling, there is a risk that the targeted removal of non-native plant species alone may not solve the problem, but only shift it to other species. When aiming for a targeted removal of non-native plant species, it is therefore important to assess which other species may take over after successful removal of the non-native species, and whether these species might create similar (or other) problems for users.

7.5. The effect of macrophyte removal on ecosystem carbon emissions is site-specific

Macrophyte removal may increase or decrease emissions of the greenhouse gasses methane (CH_4) and carbon dioxide (CO_2), and the net effect of macrophyte removal on ecosystem carbon emissions can be quick (few days to weeks after plant removal). Macrophyte life forms (i.e. if the plants grow submerged, free-floating, or emergent) and environmental parameters, including indirect effects of macrophyte removal on water temperature, as well as physical and chemical parameters in water and sediment, may explain changes in ecosystem carbon emissions after macrophyte removal.

Figure 7.5: Floating aquatic plants, such as water hyacinth (*Pontederia crassipes*) in Hartbeespoort Dam, can create dense barriers at the water surface. Bubbles of methane, which are produced in the sediment depleted of oxygen, float to the water surface and get trapped underneath the barrier created by the plants. There, bacteria can convert much of the methane to CO_2, thereby limiting methane emissions. This effect, however, can only occur when the aquatic plants create a dense barrier at the water surface.

Examples from MadMacs

- In shallow Lake Grand-Lieu, overall methane emissions were high, most likely due to a combination of muddy sediment with high amounts of organic carbon, low dissolved oxygen concentrations and high water temperatures. Methane emissions continued to be high after removal of emergent water primrose (*Ludwigia* spp.), and plant removal had no effect on total CH_4 emissions.
- Removal of submerged Nuttall's waterweed (*Elodea nuttallii*) in Lake Kemnade reduced total CH_4 emissions, but also CO_2 uptake. Both effects, however, likely only lasted for a few days to weeks. Immediately after macrophyte removal, CO_2 fixation was reduced, simply because there were much fewer aquatic plants than before the removal (plants take up CO_2 during photosynthesis; when there are fewer plants present, there is less photosynthesis, and consequently less uptake of CO_2). One week after removal, however, CO_2 fixation was back to rates recorded before the macrophyte removal. This indicates that the remaining *E. nuttallii* quickly started to regrow. The measured reduction in CH_4 emission after macrophyte removal was most likely caused by outgassing of CH_4 due to disturbance of the sediment by the mowing boat. We were not able to measure this effect directly, since sampling underneath an operating mowing boat is difficult at best. It is, however, possible that CH_4 emissions over time were in fact unaffected by the macrophyte removal, but that we were unable to capture the processes during the operation of the mowing boat correctly.
- Removal of free-floating water hyacinth (*Pontederia crassipes)* in Hartbeespoort Dam strongly increased CH_4 emissions. Likely, the free-floating vegetation before the removal acted as a barrier, which captured CH_4 and stimulated CH_4 oxidation in the rhizosphere, thereby oxidising CH_4 that was produced in the anoxic sediment underneath the plants. The removal of the barrier effect resulted in enhanced CH_4 emissions after macrophyte removal. This effect is likely to last until the macrophytes have re-grown.

Supporting information

The removal of macrophyte mass developments radically changes an ecosystem overnight, because the dominant primary producer is removed. Habitat conditions determine which group of primary producers (phytoplankton, periphyton, other macrophyte species, re-growth of the same macrophyte species) is likely to dominate after the macrophyte removal. In addition, dominance of different primary producers likely changes over time (e.g. competition between fast growing algae versus slower growing macrophytes). The nature (different types of algae, different macrophyte life-forms) and abundance of primary producers, together with environmental conditions, affect ecosystem carbon fluxes. The lack of a universal response in CH_4 and CO_2 fluxes across our case study sites suggests that both macrophyte life forms and environmental parameters are important factors determining the short-term effects of macrophyte removal on carbon fluxes. Additionally, indirect effects of macrophyte removal on water temperature and dissolved oxygen can help to explain carbon emissions.

7.6. The consequences of partial macrophyte removal on biodiversity of other aquatic organism groups are variable but generally small

Macrophyte removal disturbs the ecosystem and changes habitat structure, and this may affect the biodiversity of other aquatic organism groups and their interactions. The consequences of partial macrophyte removal on phytoplankton, zooplankton and macroinvertebrate diversity vary among sites, but often are small and short lived (few weeks). Rivers and streams generally are resilient to local disturbances so that sites from which macrophytes were removed often are recolonized within few weeks, likely from undisturbed areas upstream. The effects of macrophyte removal on lake biodiversity vary. Biodiversity of zooplankton and macroinvertebrates living within macrophytes may be negatively affected, likely due to the reduction in habitat availability, and the removal of individuals with the macrophytes. In contrast, lake phytoplankton biodiversity may increase after partial macrophyte removal. There also are some indications that fish may benefit from partial removal of macrophyte mass developments from freshwater ecosystems.

Figure 7.6a: Macrophytes are important components of freshwater ecosystems. Small fish seek shelter among the plants, and plants provide surface for the growth of periphytic algae. These algae may then be grazed upon by aquatic insects, overall leading to a diverse ecosystem. Complete removal of macrophytes will therefore likely reduce aquatic biodiversity. In contrast, we detected few and generally small effects of partial macrophyte removal on aquatic biodiversity. Photo: S. Schneider

Examples from MadMacs

- In the rivers Otra (Norway) and Spree (Germany), we observed few effects on the diversity and abundance of **phytoplankton**, **zooplankton** and **macroinvertebrates** one week after partial macrophyte removal ("partial removal" means that the removal was incomplete, and that some plants were left standing). No effects were detected six weeks after plant removal. This likely indicates that macrophyte removal indeed disturbs the ecosystem, but that rivers and streams are resilient and that sites from where macrophytes were removed are quickly recolonized, likely by passive dispersal (or drifting) from undisturbed areas upstream.
- In the lakes Grand-Lieu (France), Kemnade (Germany) and Hartbeespoort Dam (South Africa), we detected no effects of plant removal on diversity and abundance of **sediment-dwelling** macroinvertebrates. This is likely because the sediment was little disturbed by the plant removal in Lake Kemnade (where the lower 50 cm of Nuttall's waterweed (*Elodea nuttallii)* were left standing), the removal of free-floating water hyacinth (*Pontederia crassipes)* only slightly disturbed the sediment in Hartbeespoort Dam, while recolonization was rapid after removal of emergent water primrose (*Ludwigia* spp.) in Lake Grand-Lieu, possibly from nearby areas with intact native vegetation.
- One week after macrophyte removal, diversity of macroinvertebrates **living within macrophyte beds** was reduced in lakes Grand-Lieu (France), Kemnade (Germany) and Hartbeespoort Dam (South Africa), but we detected no effect six weeks after macrophyte removal. This indicates that, unsurprisingly, the removal of their habitat affects macroinvertebrates living within macrophytes, but that the remaining and re-growing plants are quickly recolonized.
- Removal of submerged Nuttall's waterweed (*Elodea nuttallii)* and emergent water primrose (*Ludwigia* spp.) reduced **zooplankton** diversity in lakes Grand-Lieu (France) and Kemnade (Germany). In Lake Kemnade, this effect was still noticeable six weeks after plant removal and may possibly be explained by a less diverse habitat for zooplankton after macrophyte removal. In contrast, removal of free-floating water hyacinth (*Pontederia crassipes)* did not affect the zooplankton living underneath the free-floating plants in Hartbeespoort Dam.
- Diversity of **phytoplankton** tended to increase after macrophyte removal in all three study lakes. This may be related to the decreased competition for light and nutrients after macrophyte removal, leading to improved conditions for phytoplankton.
- For **fish**, we found few effects of *Juncus bulbosus* removal on the behaviour of brown trout in the River Otra (Norway). If anything, brown trout used habitats from where the plants were removed more often than dense macrophyte patches. This effect may possibly be explained by the easier access to and improved visibility of drifting insects, the main food source for brown trout.

Supporting information

Interpreting biodiversity can be complicated, and both the direction of the change and desirability of that outcome can be site-specific and differ between aquatic organism groups. In MadMacs, we removed macrophytes from selected areas of public interest, in accordance with local management practices. The macrophyte removal was incomplete, i.e. macrophytes were not entirely eradicated from the ecosystem. This was because the macrophytes were only removed from selected areas of public interest while they were left standing in nearby areas, because the machines that were used for removal were not able to completely remove the plant biomass, or because lower plant parts were left standing on purpose in order to minimise sediment disturbance. In our experience, the removal practices that are applied by water managers (mowing boats, sediment harrowing) generally lead to a (temporal) increase in water turbidity, indicating that the ecosystem is being disturbed. Ecosystem disturbance may affect biodiversity positively or negatively.

In the MadMacs project, one week after macrophyte removal, we observed reduced zooplankton richness in most lakes, and reduced richness of macroinvertebrates living within macrophytes in most rivers and lakes. This is unsurprising, because the removed macrophytes were an important habitat for these aquatic organism groups, and – indeed – many of them may have been removed together with the aquatic plants. In contrast, richness of sediment-dwelling macroinvertebrates was unaffected by plant removal. This may partly be explained by the removal methods, which did not disturb the sediment strongly (for example in Hartbeespoort Dam (South Africa), the removal of free-floating *Pontederia crassipes* may not have significantly affected the sediment underneath the plants, or Lake Kemnade (Germany), where *Elodea nuttallii* was mowed to a depth of 50 cm above the sediment, a method that likely left the sediment quite undisturbed). However, we observed that removal of emergent *Ludwigia* spp. from Lake Grand-Lieu, submerged *Juncus bulbosus* in the River Otra, and several submerged macrophyte species in the River Spree, indeed did disturb the sediment. We therefore expected that the plant removal would affect sediment-dwelling macroinvertebrates. This was, however, not the case. This may possibly be explained by the incomplete removal of macrophytes from the rivers Otra and Spree (for technical reasons, a 100% removal of submerged aquatic plants from rivers is highly unrealistic), together with fast recolonization of the remaining plant parts from upstream. In Lake Grand-Lieu, the sediment-dwelling macroinvertebrates possibly rapidly recolonized from nearby plant patches. In the River Guaraguaçu (Brazil), we observed a (small) increase in shrimp abundance immediately after plant removal. Shrimp could be attracted by increased availability of detritus (which they can feed on) after plant removal.

In contrast to the other organism groups, diversity of phytoplankton tended to increase after macrophyte removal in all three study lakes. Decreased competition for light and nutrients after macrophyte removal improves conditions for phytoplankton. Such an effect did not occur in the rivers Otra or Spree, likely because the water flow generally prevents the development of site-specific phytoplankton assemblages in rivers. It is important to note, however, that increased diversity of phytoplankton is not necessarily a desirable effect, particularly when it increases along with increased biomass of phytoplankton.

Six weeks after macrophyte removal, most effects of macrophyte removal on phytoplankton, zooplankton and macroinvertebrate diversity had disappeared. This indicates that partial removal of macrophytes from selected areas of public interest generally has small long-term effects on the biodiversity of other aquatic organism groups. Partial macrophyte removal is indeed an ecosystem disturbance, but many freshwater ecosystems are resilient, and recolonization may occur within a few weeks.

It is important to note, however, that our results only apply to partial removal of macrophytes from selected areas of public interest. Partial macrophyte removal from selected areas is a common management practice in rivers and lakes where aquatic plants are perceived as a nuisance for recreational use of the water body.

Complete removal of aquatic plants from freshwater ecosystems is costly, unrealistic, and – in contrast to partial removal – may have dramatic consequences for the structure and functioning of freshwater ecosystems. In addition, regular mowing of macrophytes over several years may favour fast growing macrophyte species, and therefore – over the course of several years – lead to reduced macrophyte diversity.

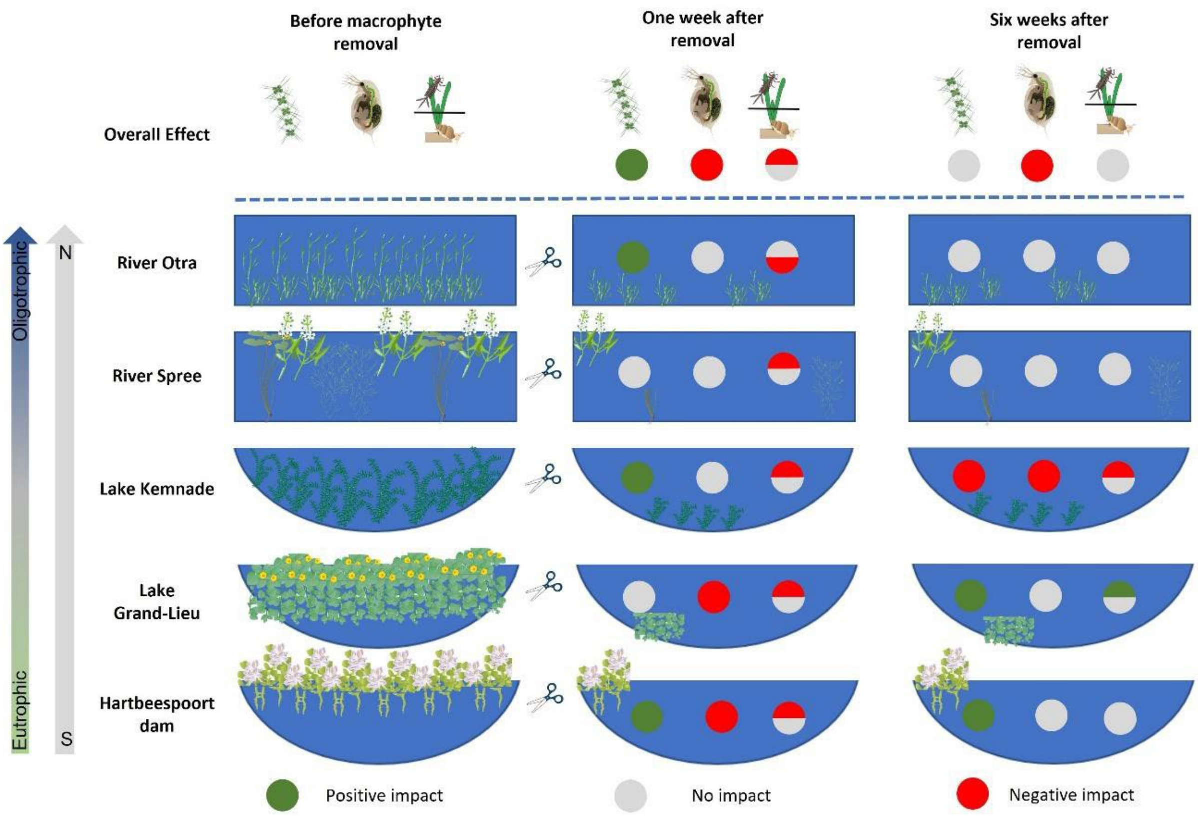

Figure 7.6b: Graphical summary of the consequences of macrophyte removal on aquatic biodiversity. From Misteli et al. (2023).

7.7. Dense stands of aquatic plants raise the water level of streams and adjacent groundwater

In rivers and streams, dense stands of aquatic plants narrow the cross-sectional area of flow and induce turbulence around stems and leaves which slow down river flow.

Therefore, dense plant stands elevate the water level at a given discharge. This impounding effect may locally increase the risk of flooding. Globally, many streams and ditches are regularly mowed to reduce the impounding effect of aquatic plants, facilitate drainage and avoid inundation. When rivers and streams have low to moderate discharge, however, aquatic plants are beneficial. By keeping the stream water level high, also the groundwater table in the adjacent floodplain is raised, thereby preventing droughts and improving nutrient and particle retention.

Figure 7.7: Dense stands of aquatic plants, e.g. water-crowfoot (*Ranunculus fluitans*; right) raise the water level in the River Spree and the groundwater table in the adjacent fields (left). This effect occurs in all rivers and streams, but the extent to which it happens depends a.o. on stream size and stream morphology, aquatic plant biomass, and aquatic plant species, and can range from negligible to several decimetres in water level rise. This impounding effect, on the one hand, may increase the risk of flooding, but on the other hand may reduce the risk of droughts. Photos: J. Köhler

Example from MadMacs

- Without aquatic vegetation, the water level is closely correlated to the present discharge. This relationship depends, e.g. on slope, roughness of the stream bed and the cross-sectional area. Therefore, the water level – discharge relationship without aquatic plants has to be established for individual sites and requires regular validation. Once established and proofed, it can be applied to periods of vegetation growth to calculate the impounding effect of these plants and the hydraulic consequences of mowing.
- We recorded river water level at 15 sites and discharge at the beginning and end of a 32 km section of the River Spree upstream of Berlin, Germany, for several years. We used the difference between the depth-discharge relationship in the presence (growing season) and absence (winter) of aquatic plants to quantify this impounding effect on water level. Using these data, we modelled mean depth, mean velocity of flow, and gas exchange.
- On average (June-August, 2019), rooted aquatic plants elevated the mean water depth from 90 to 120 cm, slowed down the mean velocity of flow by 35%, extended the time of flow along the river section accordingly and reduced the intensity of gas exchange between water and air by about 40%.
- River and groundwater at the adjacent floodplain were closely connected. Changes in river water level propagated within a few hours to the groundwater. Therefore, the impounding effect of aquatic plants in the river kept the groundwater level at a higher level and reduced mineralization (and thus nutrient release) of adjacent fens.

Supporting information

Dense mats of aquatic vegetation generally raise the water level in streams. The extent, however, depends on river size and morphology, aquatic plant biomass, and aquatic plant species, and can range from negligible to several decimetres in water level rise.

7.8. Nobody likes macrophyte mass developments, but visitors tend to regard them as less of a nuisance than residents

Overall, the majority of visitors and residents in the surrounds of a water body with dense aquatic vegetation perceive the aquatic plants 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. The denser the macrophytes are, the more they are perceived as a nuisance. Residents are likely to perceive macrophyte mass developments equally negative or worse than do visitors, and the biggest differences tended to occur at sites where boating was an important recreational activity for residents.

Figure 7.8a: Macrophyte mass developments clog boat propellers, are cumbersome for swimmers, and generally make boating difficult (e.g. top right, where a boat is stuck in water hyacinth on Hartbeespoort Dam). Overall, dense aquatic vegetation negatively affects the value of the water body for active recreation, and we speculate that residents build up a negative perception of the plants over time. Photos (from left to right and top to bottom): S. Schneider, J. Coetzee, S. Hilt, Limnologische Station Iffeldorf

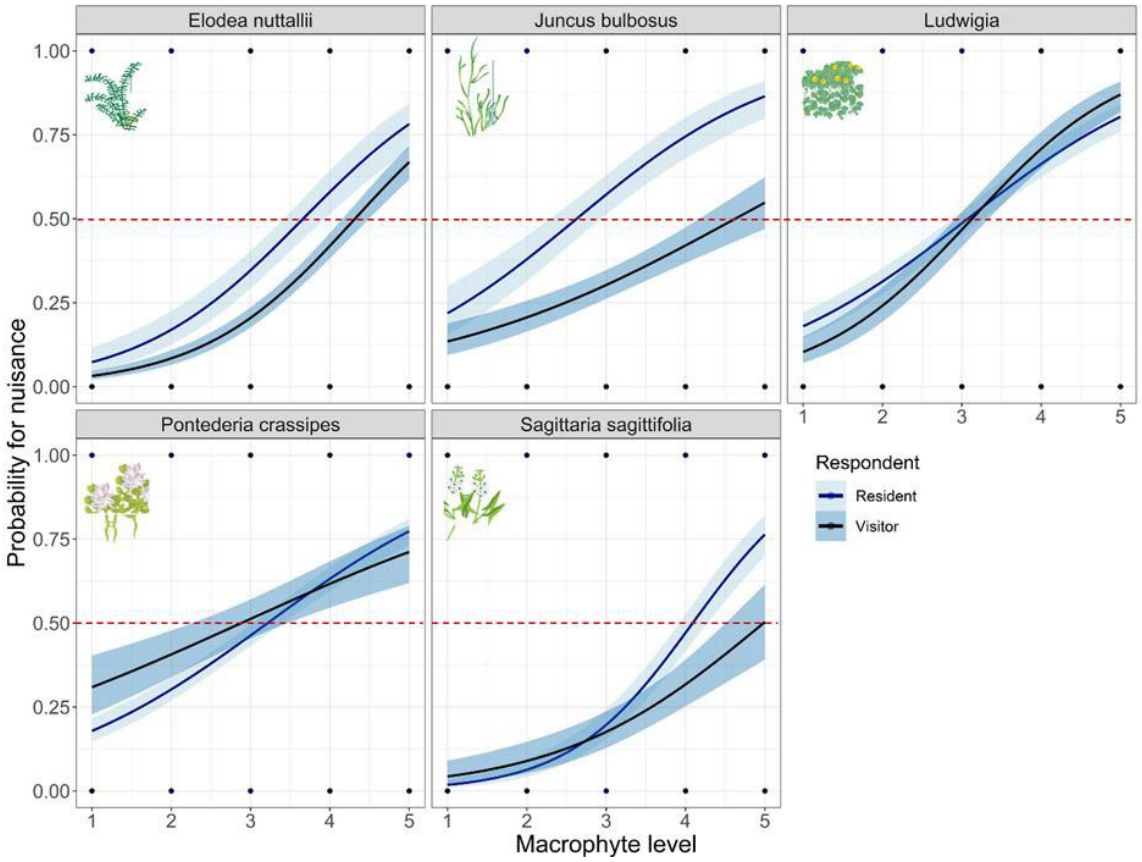

Figure 7.8b: Probability of perceived nuisance in relation to macrophyte growth level (1: few aquatic plants -5: massive plant growth), macrophyte species and respondent types (resident and visitor) (GLMMs). Bands are confidence intervals (0.95). The red dashed line represents the level at which probability of nuisance is 50%. From Thiemer et al. in press. Underlying drivers for perceived nuisance growth of aquatic plants. Environmental Management.

Examples from MadMacs

- 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. The River Otra and Lake Kemnade are intensively used by residents for boating. These activities need 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 the visitors perceived the mass development of native aquatic plants as nuisance. Both groups expressed concerns about biodiversity most often. Residents were more concerned about the effect of the mass development on biodiversity than visitors, and residents perceived high plant biomasses as more negative for angling. The reasons for this are, however, unclear.
- In Hartbeespoort Dam (South Africa), a very high percentage of both visitors and residents (more than 90%) perceived the mass development of water hyacinth *(Pontederia crassipes)* as nuisance. People were most concerned about biodiversity, followed by boating and the beauty of the landscape. Hartbeespoort Dam is one of few freshwater bodies which are available for recreation in South Africa, and water hyacinth at this site has been perceived as problematic for decades. The high perception as nuisance, and the absence of a difference between residents and visitors might therefore be related to the fact that people across the entire country have been well aware of the continued struggle against water hyacinth for decades, combined with the high relevance of this water body for the entire country.
- 75% of both residents and visitors at Lake Grand Lieu (France) 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 beauty, its value for biodiversity and for birdwatching. The absence of a difference between residents and visitors, and the relatively low perception as nuisance among the residents compared to other sites, might be explained by the low importance of active recreation on the lake.

Supporting information

Our data suggest that the biggest conflicts of interest are likely to arise when high biomasses of aquatic vegetation occur in water bodies which residents want to use for active recreation. This should be considered when regulating rivers and lakes, because regulation may turn water bodies into a “perfect habitat” for aquatic plants (see key message #1). “Promises” that residents will be able to use a newly created or modified water body for active recreation may be difficult to keep if the new water body is shallow, nutrient rich, and experiences little disturbance (see key messages # 1 and 2). Mass developments of aquatic plants are likely to lead to complaints, first and foremost among the residents that used to use (e.g. River Otra), or want to use (e.g. Lake Kemnade), the water body for active recreation.

7.9. Aquatic plant management often does not affect overall societal value of the ecosystem

When quantified on a monetary basis, recreation, including passive recreation (i.e. walking, relaxing, picnicking or similar activities on the banks of rivers or lakes), is often the most important societal use of water bodies experiencing macrophyte mass developments.

Nevertheless, macrophyte removal often has little effect on the summed economic value of the different societal uses. This is because passive recreation, which often dominates total economic value, is largely unaffected by aquatic plants, and because benefits of aquatic plant removal for active recreation on the water can be offset by disbenefits for biodiversity.

Exceptions may be water bodies with high visitor densities where the visitors perceive the plants as “ugly”. At such sites, macrophyte mass development not only interferes with active recreation on the water, but also with recreation along the banks. In such cases, the “do-nothing option”, i.e. leaving the macrophytes standing, clearly reduces the summed societal benefits. In many cases, however, the “do-nothing” option has little effect on the summed value of societal benefits. An important message for management is to consider the aesthetic appreciation by different categories of recreative users before engaging in costly removal.

Figure 7.9: Macrophyte mass developments negatively affect active recreation, and some visitors perceive the aquatic plants as “ugly”. This negative perception may affect passive recreation activities, e.g. relaxing on the banks (here: Hartbeespoort Dam (top) and Lake Kemnade (bottom), and thereby affect the societal value of a water body. Photos: S.F. Harpenslager (top), S. Zeisig (bottom)

Examples from MadMacs

- Total economic value of all five case study sites was dominated by different forms of recreation.
- Lake Kemnade had the highest total estimated value, mainly due to the large number of visitors from the surrounding Rührgebiet that engaged in walking, picnicking or similar activities on its banks throughout the year. The members of active sailing and angling clubs were small compared to the high numbers of "passive" visitors.
- The River Spree had the most diverse portfolio of uses. Despite its location near the city of Berlin, the total number of residents and visitors engaged in recreation was much lower than in Lake Kemnade (the other MadMacs case study in Germany) – likely due to the availability of many more alternatives around Berlin.
- The strict nature reserve of Lake Grand-Lieu had a low estimated total economic value due to the limited access, although the marginal zone attracts recreation, also from the nearby city of Nantes. Likely, the nearby Atlantic coast offers an attractive alternative for recreation.
- In four out of our five case study sites, **maximum plant removal** (i.e. the maximum plant removal theoretically feasible at each site) did not increase total economic value by more than 10% (and often had no clear effect at all). This was because (i) passive recreation was little affected by plant removal (Lake Grand Lieu), (ii) aquatic plants are an important habitat for many organisms, and maximum removal reduced the availability of this important habitat below the optimum for fish, hence reducing angling value (River Otra), (iii) a falling groundwater level in the floodplain indeed improved productivity of fodder but at the same time reduced wetland biodiversity (River Spree), and (iv) **active** recreation on the water indeed would benefit by maximum plant removal but its importance is less than **passive** recreation on the banks, the latter being unaffected by removing more aquatic plants compared to the current management regime (Lake Kemnade).
- In Hartbeespoort Dam, maximum plant removal likely indeed would increase the estimated total economic value, because the value of boating, angling and passive recreation would increase after plant removal. Mitigating the disadvantage of plant removal (increased risk of toxic cyanobacterial blooms) would cost less than the increase in recreative value.
- In three out of our five case studies, the **"do-nothing"** option did not decrease total economic value by more than 10% of its current value. This was because (i) in Lake Grand-Lieu passive recreation is unaffected by the presence of the plants, and the presence of water primrose (*Ludwigia* spp.) indeed reduces the area and value of fodder production in the floodplain, but not by much, (ii) in the River Otra, plants are currently only removed from a few selected areas, hence weed cover would not increase greatly if plant removal was stopped and therefore had no great effects, and (iii) in the River Spree, doing "nothing" indeed would reduce the value the river has for boating, angling and floodplain fodder production, but due to the overruling dominance of passive recreation, this would be less than 10%.
- In contrast, a Lake Kemnade visibly fully filled with Nuttall's waterweed (*Elodea nuttallii*) appeared a much less pleasant destination for a walk or a picnic as its aesthetic appreciation declined markedly compared to the current condition where the plants are not yet fully visible, thereby reducing the total economic value in a "do-nothing" regime.
- In Hartbeespoort Dam, all forms of recreation declined under a do-nothing management regime where water hyacinth cover increases to 50% of the dam's surface, thereby reducing its economic value.

Supporting information

We used the ecosystem services framework to get monetary value estimates for each type of use. These estimates can be expressed in Euro per hectare per year and added to a sum called “Total Economic Value” (TEV). Such a monetary value estimate does not necessarily imply that distinct markets exist for all these services, but it suggests the importance of the service to people in an objective way. We quantified a large number of services but their contribution to the total value was often very limited. Examples are food and fodder production in the floodplain of rivers and along the banks of lakes, carbon retention for greenhouse gas mitigation, nutrient retention for downstream water quality improvement, or the provision of irrigation water to downstream agriculture. We also included “non-use” for biodiversity conservation.

Macrophyte mass developments interfere with activities such as boating, angling or swimming, and perceived nuisance often is the main reason for macrophyte removal from freshwater ecosystems. In addition, macrophyte mass developments also may affect other uses of the ecosystem, such as food or drinking water provision, and flood or erosion prevention. Macrophyte removal, however, may also have undesired side-effects (e.g. algal blooms, see key message #3) which in turn affect societal use of the ecosystem. For each of our case study sites, we quantified all societal uses on a monetary basis, and found that, overall, recreation clearly was most important. This included both active (swimming, boating, angling) and passive recreation (walking the banks, relaxing). The importance of the other uses varied among our case study sites.

We derived two strongly contrasting management regimes (“do-nothing”, i.e. leave the macrophytes standing and “maximum removal”) to bring our ecosystem services framework to “its maximum”. We compared these regimes with “current practice” and found that they often had little effect on the summed value of the different uses. Only Lake Kemnade and Hartbeespoort Dam were exceptions. Both have high visitor densities, and these visitors will perceive the plants as “ugly” once the lake will to a large degree be visibly filled with aquatic plants, which is the case for the “do-nothing” option. For this reason, the massive amounts of aquatic plants also negatively affect more passive forms of recreation along the banks (e.g. walking, relaxing).

In Hartbeespoort Dam, toxic cyanobacteria are likely to develop after maximum aquatic plant removal. However, the cost of treatment for drinking water production reported in literature is not particularly high compared to the societal benefits. Still, cyanobacterial blooms should not be ignored as a potential undesired side-effect.

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