Causes of macrophyte mass development and recommendations for managing water courses with dense aquatic vegetation

- key messages from the MadMacs project –

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Summary

In the project “Mass development of aquatic macrophytes; causes and consequences of macrophyte removal for ecosystem structure, function, and services” (MadMacs), we studied six sites in rivers and lakes with mass development of macrophytes. The sites were located in Norway, Germany, France, South Africa, and Brazil, and the macrophytes were perceived as problematic by water managers and residents. At each site, we – in collaboration with local water managers – mechanically removed the macrophytes from areas ranging from 550 m^2 (Lake Grand Lieu) to 70,000 m^2 (River Spree), reflecting current management practices. We quantified the short-term consequences (up to six weeks) of macrophyte removal on biogeochemistry and biodiversity, comparing each macrophyte removal site with a nearby site in which the macrophytes were left standing. We distributed questionnaires, in which we asked residents and tourists how they perceive the aquatic vegetation. We also quantified ecosystem services and compared the current situation with management regimes where the macrophytes were fully removed, as well as with a “do-nothing” scenario, i.e. where the macrophytes were left standing.

Overall, we learned the following lessons:

- Mass developments of macrophytes often occur 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 the biodiversity of other aquatic organism groups are variable but generally small
- Dense stands of macrophytes raise the water level of streams and adjacent groundwater
- Nobody likes macrophyte mass developments, but visitors tend to regard them as less of a nuisance than residents do
- Aquatic plant management often does not affect overall societal value of the ecosystem much

Introduction

Large aquatic plants growing in rivers or lakes are usually called “macrophytes”. The term “macrophytes” includes aquatic flowering plants and ferns, aquatic mosses, and some larger algae that have tissues that are easily visible. Macrophytes, like all other plants, use the sun’s energy to convert carbon dioxide into energy (biomass). Macrophytes come in a variety of forms and shapes and are generally categorized into four groups: emergent (rooted under water with top parts above the water surface), floating-leaved (rooted under water with leaves floating on the water surface), submerged (grow entirely underwater) and free-floating (floating plants not attached to the sediment).

Fig. 1. *Mass developments of macrophytes occur worldwide and are often perceived as a nuisance. We studied (from top to bottom, and left to right) (i) bulbous rush (*Juncus bulbosus*) in the River Otra (Norway), (ii) several species of native macrophytes in the River Spree (Germany), (iii) tanner grass (*Urochloa arrecta*) in the River Guaraguaçu (Brazil), (iv) Nuttall’s waterweed* (Elodea nuttallii*) in Lake Kemnade (Germany), (v) water primrose* (Ludwigia sp.) *in Lake Grand-Lieu (France) and (vi) water hyacinth (*Pontederia crassipes*) in Hartbeespoort dam (South Africa). Photos: S. Schneider, J. Köhler, A. Padial, S. Hilt, B. Misteli, A. Petruzzella*

In the project “Mass development of aquatic macrophytes; causes and consequences of macrophyte removal for ecosystem structure, function, and services” (MadMacs; https://www.niva.no/en/projectweb/madmacs), we studied six sites in rivers and lakes with mass development of macrophytes. The sites were located in Norway, Germany, France, South Africa and Brazil, and the macrophytes were perceived as problematic by water managers and residents. At each site, we – in collaboration with local water managers – mechanically removed the macrophytes from areas ranging from 70,000 m^2 (River Spree) to 550 m^2 (Lake Grand Lieu), reflecting current management practices. We quantified the short-term consequences (up to six weeks) of macrophyte removal on biogeochemistry and biodiversity, comparing each site from which the macrophytes were removed with a nearby site in which the macrophytes were left standing. We distributed questionnaires, in which we asked residents and tourists how they perceive the aquatic vegetation. We also quantified ecosystem services and compared the current situation with management regimes where the macrophytes were fully removed, as well as with a “do-nothing” scenario, i.e. where the macrophytes were left standing.

Overall, we learned the following lessons:

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.

Fig. 2. *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 centre 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.

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.

Fig. 3. *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

In our experience, 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.

3) Macrophyte removal treats the symptom rather than the cause

The underlying reasons for the mass development of aquatic plants generally are 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.

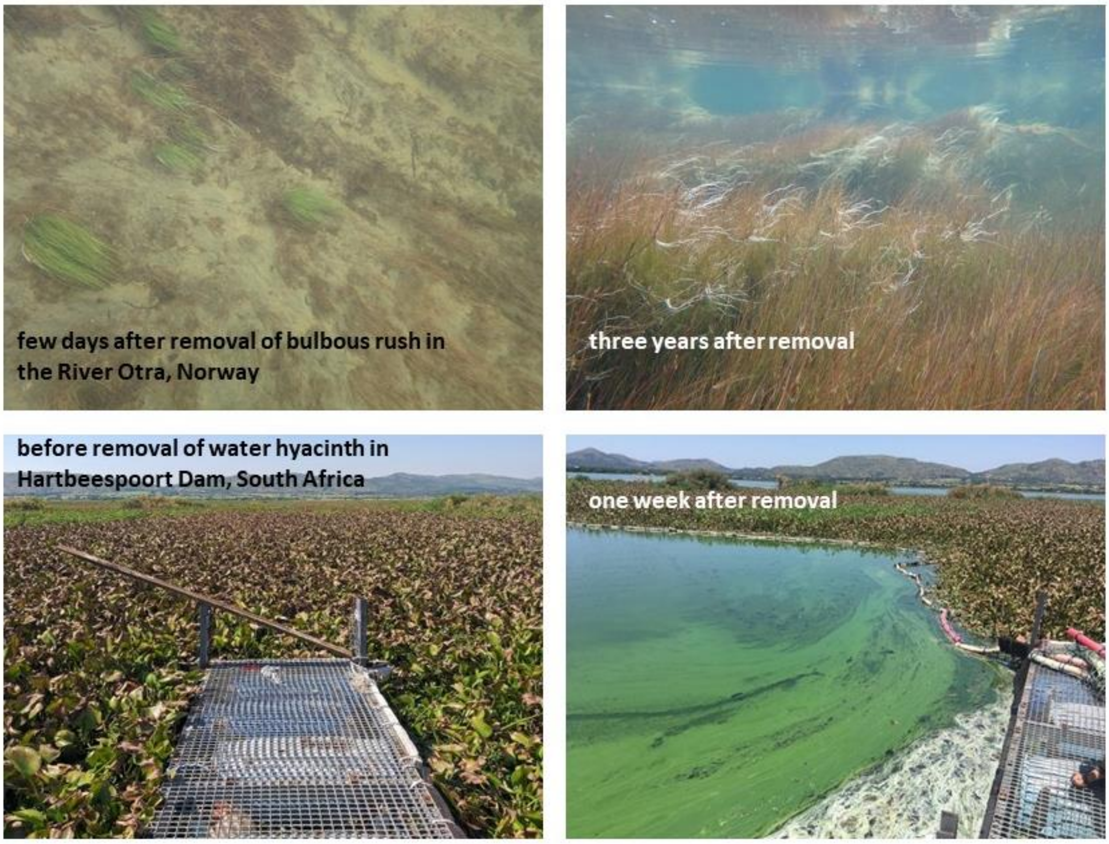

Fig. 4. *Plant cutting followed by sediment harrowing significantly reduced the biomass of bulbous rush (*Juncus bulbosus*) in the River Otra, but some plants remained (top left). Three years after the mechanical removal, the plant biomass had fully regrown (top right). In nutrient-rich ecosystems, plant 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 reasons for the massive macrophyte development are not mitigated, plant regrowth commonly occurs after mechanical plant removal.

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.

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.

Fig. 5. *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, 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 shift the problem of perceived nuisance growth to another species, rather than solve it.

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.

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.

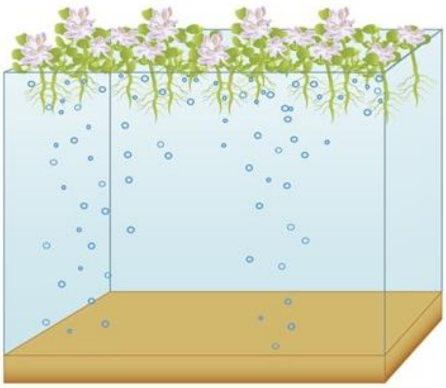

Fig. 6. *Floating aquatic plants, such as water hyacinth (*Pontederia crassipes*) in Hartbeespoort Dam, can create dense barriers at the water surface. Bubbles of methane, which are produced in the sediment depleted of oxygen, float to the water surface and get trapped underneath the barrier created 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.

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.

Fig. 7. *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 i*n 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.

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.

Fig. 8. *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

- In the River Spree (Germany), rooted aquatic plants elevated the mean water depth from 90 to 120 cm, and slowed down the mean velocity of flow by 35%.
- The water depth in the River Spree was closely connected to the groundwater in the adjacent floodplain. Changes in river water depth propagated within a few hours to the groundwater. Therefore, the impounding effect of aquatic plants in the river kept the groundwater 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.

8) Nobody likes macrophyte mass developments, but visitors tend to regard them as less of a nuisance than residents do

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 more dense 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.

Fig. 9. 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

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.

9) Aquatic plant management often does not affect overall societal value of the ecosystem much

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.

Fig. 10. 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 Ruhrgebiet 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.