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Mass development of monospecific submerged macrophyte vegetation after the restoration of shallow lakes: Roles of light, sediment nutrient levels, and propagule density

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ABSTRACT

After restoration, eutrophicated shallow freshwaters may show mass development of only one or two submerged macrophyte species, lowering biodiversity and hampering recreation. It is unclear which environmental factors govern this high percentage of the volume inhabited (PVI[2]) by submerged macrophytes, and whether the development of a more diverse, low canopy vegetation is likely to occur if dominant species decline in abundance.

We hypothesized that (1) adequate light and high sediment nutrient availability leads to massive development of submerged macrophytes, and (2) that macrophyte species richness is low at high PVI, but that this is not caused by a lack of viable propagules of non-dominant species (especially charophytes).

To test these hypotheses, fifteen shallow waters in the Netherlands were studied with respect to submerged vegetation (including propagules), water, and sediment characteristics.

The probability of high submerged macrophyte PVI is highest in shallow waters where light availability in the water layer and phosphorus availability in the sediment are abundant. These conditions typically occur upon restoration of eutrophic waterbodies by reducing water nutrient loading or applying biomanipulation. Other factors, as top-down control, can additionally influence realised PVI. Viable propagules of species other than the dominant ones, including charophytes, were found in most of the sediments, indicating that once the dominant species declines, there is local potential for a diverse submerged vegetation to develop. Results can be used to predict when mass development occurs and to tackle the factors causing mass development.

1. Introduction

Shallow waters worldwide suffer from high anthropogenic nutrient input leading to loss of submerged macrophytes by dominance of floating macrophytes, algae or cyanobacteria. Submerged macrophytes are key players in these ecosystems, because they provide a positive feedback for a clear water state and enhance biodiversity (Carpenter and Lodge, 1986). A wide variety of restoration measures have been taken to restore water transparency and submerged macrophyte vegetation in eutrophicated lakes, in particular through the reduction of external nutrient input and the removal of zooplanktivorous and sediment disturbing fish (i.e. biomanipulation) (Gulati and Van Donk, 2002; Jeppesen et al., 2007). After successful restoration of water transparency, a diverse vegetation of submerged macrophytes can reappear (Bakker et al., 2013; Pot and Ter Heerdt, 2014).

The restoration of clear water in eutrophicated lakes may also lead to massive development of submerged macrophytes, which is often characterised by monospecific stands of eutrophic vascular species with a vertical growth strategy and surface canopy formation, leading to a high percentage of volume inhabited (PVI[3]) in the water column (Hilt et al., 2006; Lamers et al., 2012). These massive stands of tall submerged macrophytes can prevent the development of a more diverse

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[2] PVI: The percent of the water volume inhabited by submerged macrophytes.
[3] PVI: The percent of the water volume inhabited by submerged macrophytes.

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vegetation by being superior competitors for light and space over slower growing species, especially isoetid and charophyte species. Additionally, mass development of submerged macrophytes can cause problems for human use of lakes, for example for recreation and navigation (Zehnsdorf et al., 2015). It is, however, unclear whether these large macrophyte stands are always species poor, or whether other species may still be present below the canopy of the dominant species. It is also unclear whether there is local potential for a more diverse and low-growing vegetation to develop in these ecosystems. In particular the development of charophytes is of interest in this respect, because they maintain low canopies that cause less interference with human use of lakes (e.g. Van Nes et al., 2002a). Charophytes are additionally favoured by water managers because they are promotors of good water quality (Bakker et al., 2010; Blindow et al., 2014), they can maintain large and long-lived propagule banks (Bakker et al., 2013), and they are rapid colonizers of new or restored water bodies (Noordhuis et al., 2002; Pot and Ter Heerdt, 2014). Charophyte species can in principle be a dominant component of a stable clear water state in eutrophic shallow lakes (Van Nes et al., 2002b).

The exact size of the macrophyte stand at which it causes problems depends on the specific ecosystem service provided by the lake (Mitchell, 1996). We will therefore not use a single threshold level to describe problematic stands, but will investigate which factors influence submerged macrophyte PVI in general under field conditions. Both light energy (photosynthetically active radiation, PAR) and nutrient availability highly influence the growth and abundance of autotrophs, including submerged macrophytes (Bornette and Puijalon, 2011). Light availability for the plants can be reduced for example by phytoplankton growth in the water column or by periphyton growth on the macrophytes (Hilt et al., 2006; Bornette and Puijalon, 2011; Phillips et al., 2016). Restoration measures are often aimed at improving light availability (Bakker et al., 2013). An often-overlooked component that may determine whether mass development of macrophytes occurs after water clarity has been restored is sediment nutrient availability (e.g. Bachmann et al., 2002; Eigemann et al., 2016). Rooted submerged macrophytes are able to acquire nutrients from the sediment (Carignan and Kalff, 1980; Halbedel, 2016). Generally, high abundance of macrophytes in the water column, expressed as PVI, may thus occur more frequently at high sediment nutrient conditions (Barko et al., 1991; Carr and Chambers, 1998; Fig. 1). Indeed, laboratory growth experiments have shown that submerged macrophyte species grow faster or taller at increasing sediment nutrient concentrations (e.g. Barko and Smart, 1986; Angelstein et al., 2009; Martin and Coetzee, 2014). However, to our knowledge, field evidence is still largely lacking (Bachmann et al., 2002).

In this study, we hypothesised that: (1) high submerged macrophyte

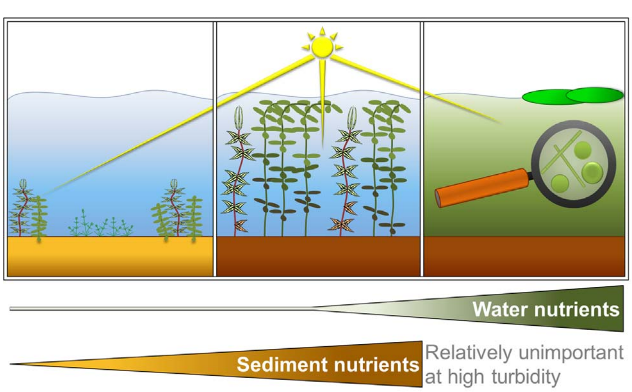

Fig. 1. Theoretical relashionship between submerged plant PVI and sediment nutrient levels. At increasing nutrient availability, submerged macrophyte PVI increases, but diversity decreases. At high water turbidity, for example by high water nutrient load, submerged macrophytes are inhibited irrespective of sediment nutrient levels.
Figure is adapted from Lamers et al. (2012): Fig. 1.

PVI will occur when sufficient light is available for submerged macrophytes to germinate and grow, and sediment nutrient availability supports high growth rates. (2) Massive stands of submerged macrophytes will consist of a lower number of plant species than stands with lower PVI, but viable propagules of species other than the dominant species will be present in the sediment top layer below massive stands, especially from charophyte species.

To test these hypotheses, we measured vegetation and environmental parameters and sampled the propagule bank in shallow lakes and ponds in the Netherlands, varying in submerged macrophyte abundance, throughout the growing season. We focused on both N and P in the nutrient analyses, because they are both considered to be key nutrients in determining the growth of photoautotrophs in shallow lakes (Moss et al., 2013).

2. Methods

2.1. Study sites

We selected 15 shallow lakes and ponds throughout the Netherlands that were eutrophicated and have undergone restoration management and/or experienced problems with massive stands of submerged vegetation (see Table 1 & Appendix A Table A1 for restoration methods applied and study site characteristics). Most of the intensive restoration measures have taken place many years ago and will therefore not have influenced the amount of submerged plants present directly, but only indirectly via the abiotic conditions as a result of the management. Most of these abiotic conditions are measured in this study. In several lakes, submerged plants are still harvested locally, but these harvested sites were avoided in our study. The surveyed aquatic ecosystems can be characterized as meso- to eutrophic (based on surface water nutrient concentrations) water with moderate to high surface water alkalinity and pH (lake average alkalinities: 1.4–4.6 meq L^{-1} and daytime pH: 8.3–9.6). Total P in the surface water averaged (± SE) 0.13 ± 0.03 mg P L^{-1}, whereas total N averaged 0.31 ± 0.03 mg N L^{-1} in sites with submerged macrophytes. In sites without submerged macrophytes, total P and N in the surface water averaged 0.09 ± 0.01 and 0.59 ± 0.05 mg L^{-1}, respectively.

We selected four sites per ecosystem using the following two criteria: (1) they should be situated in open water, where water depth is between 1 and 1.5 m and (2) their position in the waterbody is most northern (N), eastern (E), southern (S) or western (W), respectively for each site. We avoided areas with apparent direct anthropogenic disturbance including: macrophyte mowing sites, harbours, navigation channels, and areas close to beaches or fishing locations. Sites heavily shaded by large shoreline trees were also avoided.

Because vegetation was expected to vary not only spatially, but also temporally within an ecosystem, sites were visited three times throughout the growing season, using a small flat-bottomed boat. All sites were visited in three rounds: from May 13 until June 26, from July 8 until August 15, and from August 21 to October 4, using a high-sensitivity GPS device to determine each location (eTrex® H., Garmin Ltd., Southampton, UK).

2.2. Macrophyte survey

At each site we measured water depth and depth of the submerged macrophyte canopy below the water surface (hereafter referred to as 'canopy depth'), from which submerged macrophyte height was calculated (water depth – canopy depth). We visually estimated total cover (%) and relative abundance per species (%) at four spots around the perimeter of the boat using an aquascope (also known as a bathyscope). This resulted in a survey area of approximately 10–15 m^2 per site. We used submerged macrophyte height and cover, together with water depth, to calculate PVI. To account for possible rare species present underneath the dominant vegetation, we additionally