



Submerged macrophyte decline in shallow lakes: What have we learnt in the last forty years? ☆



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ABSTRACT

Over the last 40 years there has been substantial evidence that high biomasses of submerged aquatic plants and phytoplankton rarely occur together in shallow lakes, but it is clear that when present, plants have a competitive advantage over algae.

Aquatic plants provide habitat structure, which influences the fish community such that zooplankton and other macroinvertebrates maintain a top-down control on algal growth, and this control is largely independent of the nutrient supply to the lake. Nonetheless it is clear that many, but not all, lakes lose their vegetation as nutrient loading increases. However, in eutrophic lakes, the subsequent dominance by phytoplankton is more likely to be a result of the loss of vegetation rather than the cause.

At higher nutrient levels, grazing or mechanical damage can reduce plant cover allowing rapid development of algae. Changes to fish community structure or the influence of toxic chemicals can reduce invertebrate algal grazers, overcoming the positive feedback loops that stabilise the plant dominance.

The longer-term stability of macrophyte dominance is also reduced if there are few surviving plant species. Such loss of species richness is associated with increased nitrogen loading. Submerged plants also depend on a spring clear-water phase to become established, and local weather conditions during winter and spring may determine the relative success of phytoplankton and plant growth, leading to a progressively longer period of algal dominance and fewer surviving plant species.

The loss of submerged vegetation from lakes, although often perceived as a rapid change, is more likely to be the final conclusion of a process in which the competitive advantage of a diverse plant community is eroded by many pressures that are collectively interpreted as eutrophication.

In attempts to manage our environment we hope to find simple, closed stable systems that will respond to measures designed to meet our perceptions of improved ecological quality. What we increasingly find are more complex open systems, which do not necessarily respond as expected. We look for simple and widely applicable explanations where none are likely to exist.

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1. Introduction

Forty years ago, ecological studies of shallow lakes intensified in response to the growing problems arising from eutrophication. A particular concern at that time, at least in the UK, was the obvious loss of submerged aquatic vegetation, its replacement by phytoplankton and the resulting loss of invertebrate diversity (Morgan, 1970; Mason and Bryant, 1975; Phillips et al., 1978). Macrophyte loss is now clearly recognised as being intimately linked with eutrophication, particularly in shallow lakes where the photic zone

extends over the majority of the bed, (Hargeby et al., 1994; Blindow et al., 2006) and many attempts have been made to reverse this process (Moss, 1983; Moss et al., 1996a; Hilt et al., 2006; Søndergaard et al., 2007). The success of lake restoration is often judged by how rapidly macrophytes return, yet we still struggle to elucidate the ecological mechanisms for either the initial decline of macrophytes or their frequently slow response to nutrient reduction (Lauridsen et al., 2003; Søndergaard et al., 2007; Bakker et al., 2012).

It was early recognised that in very shallow lakes it might not be easy to account for macrophyte loss simply through increased competition for light as a result of phytoplankton growth, and a model was therefore proposed where increased periphyton growth initially suppressed plant growth, with phytoplankton subsequently becoming dominant (Phillips et al., 1978). This hypothesis pre-dated the idea of alternative equilibria that has become so

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important in understanding shallow lake systems (Uhlmann, 1980; Irvine et al., 1989; Scheffer et al., 1993), but it was a perhaps an augury of the concept, as it assigned macrophytes to a central stabilising role in the functioning of shallow lakes. What has emerged over the last forty years is a clearer understanding of how macrophytes influence the ecology of shallow lakes, in particular the positive feedback systems that maintain what are now widely recognised as the alternative stable states of macrophyte-dominated clear water and plankton-dominated turbid water (Jeppesen et al., 1998b; Burks et al., 2006).

When present, extensive macrophyte beds sequester nutrients (Blindow, 1992b; Ozimek et al., 1993; Van-Donk et al., 1993; Kufel and Kufel, 2002), provide refuges from visual predators on grazing zooplankton (Timms and Moss, 1984; Schriver et al., 1995), and may produce allelopathic exudates (Van Donk and Van de Bund, 2002; Gross et al., 2007), all of which mitigate against phytoplankton growth and thus maintain clear water conditions (Fig. 1). Conversely, when macrophytes are absent, small planktivorous fish reduce zooplankton grazing, and, free of the influence of visual predators in the increasingly turbid water, can reach high densities thus promoting phytoplankton dominance (Jeppesen et al., 1997). Numerous studies have demonstrated that these alternative states can exist over a relatively wide range of nutrient conditions (Leah et al., 1980; Balls et al., 1989; Irvine et al., 1989; Jeppesen et al., 2000; Jeppesen et al., 2003). Clear water and macrophyte-dominance conventionally define the initial state of unimpacted shallow lakes, though whether this is truly a 'reference' state, or merely one that reflects the shifting baseline effect of drift in perception, is a moot point. There are indications that prior to expansion of human populations and depletion of large, nutrient-redistributing grazing herds, some shallow lakes may naturally have been rich in nutrients and have had characteristics that we would now see as detrimental (Moss, 2015). It is clear, nonetheless, that most become plankton dominated under the pressure of nutrient addition, whether natural or artificial, while current aims of conservation philosophy, which are perhaps more focused on issues of biodiversity than ecological processes, are to maintain clear water with low-moderate nutrient concentrations in which a high diversity and cover of macrophytes can thrive. In this review, we summarise what we have learnt over the last 40 years about the mechanisms that overcome the apparent stability of this system to allow phytoplankton to become dominant, and how this should influence our approach to restoration.

2. Light availability and competition with algae

While at a very broad geographic scale, the proportion of lakes dominated by submerged macrophytes clearly decreases with increases in total phosphorus (TP) and total nitrogen (TN), logistic models quantifying this relationship show wide variation, which can be linked, through climatic differences, to the relative production of algal biomass and water depth, suggesting that light may still be a key issue (Kosten et al., 2009). Early reports of macrophyte loss following eutrophication assumed this was a consequence of reduced light availability caused by phytoplankton development (Mason and Bryant, 1975), as it had already been established by correlation that in deep lakes light was a key factor influencing the depth distribution of macrophytes (Spence and Chrystal, 1970). This nutrient-chlorophyll-light relationship remains true (Chambers and Kalff, 1985; Sand-Jensen and Madsen, 1991; Middelboe and Markager, 1997), although the relationship between the maximum colonised depth of macrophytes and nutrient concentrations is weak, not least because of the influence of coloured dissolved organic sub-

stances and suspended inorganic matter, whose concentrations are largely independent of nutrients. This suggests a more complex relationship linking nutrients to the distribution and development of macrophytes (Søndergaard et al., 2013) and one which does not necessarily assume that the loss of macrophytes is consequential on nutrient increase and phytoplankton development.

In 1978, Phillips et al. pointed out that in very shallow lakes, phytoplankton growth may not reduce light sufficiently to prevent the growth of submerged macrophytes and suggested that shading by epiphytic algae was the primary factor causing macrophyte decline. Since then, the capacity for epiphytic algal growth to reduce light availability has been confirmed (Sand-Jensen and Borum, 1991) and thus to reduce macrophyte growth (Sand-Jensen and Søndergaard, 1981; Daldorph and Thomas, 1995; Jones et al., 1999; Roberts et al., 2003). The impact of epiphytes (or periphyton, as a common term for all attached living and dead material), is particularly important in shallow water, where the relative effect of light attenuation by phytoplankton is lower. For example, the epiphyte community that developed on *Lobelia dortmanna* attenuated the incident light in spring by between 67 and 82%, substantially reducing growth and maximum depth of colonisation from 3.5 to 1.0 m (Sand-Jensen and Borum, 1984).

The relationship between nutrients and periphyton in lakes is, however, variable. Some studies demonstrate an increase of periphyton with nutrients (Moss, 1976; Eminson and Phillips, 1978; Cattaneo and Kalff, 1980; Eminson and Moss, 1980; Jones et al., 1999, 2000; Bécares et al., 2007; Beresford and Jones, 2010) and a greater response than phytoplankton (Sand-Jensen and Søndergaard, 1981). However, others only found an impact of nutrients when fish were present (Mazumder et al., 1989) or no relationship (Lalonde and Downing, 1991; Lambert et al., 2008). Using experimental ponds, Jones et al. (2002) found that periphyton abundance on the surface of plants was controlled by the density of grazing invertebrates rather than nutrient load, confirming previous experimental studies which have demonstrated the beneficial impact of snails on submerged macrophyte growth via the removal of epiphytes (Brönmark, 1985; Underwood, 1991; Underwood et al., 1992).

Predatory fish influence densities of benthic invertebrates in lakes (Brönmark et al., 1992; Diehl and Kornijow, 1998), though probably not to the same extent that they influence populations of zooplankters in the much less structured open water environment (e.g. compare Moss et al. (1998) and Kornijow et al. (2016)). Experimental manipulation of fish has demonstrated that in enclosures devoid of molluscivorous (e.g. *Lepomis microlophus*) or benthivorous (e.g. *Tinca tinca*) fish, invertebrate grazers increased, reducing periphyton and increasing macrophyte biomass (Martin et al., 1992; Brönmark, 1994). Direct manipulation of invertebrate (snail) densities produces similar results (Underwood, 1991; Underwood et al., 1992). Elger et al. (2009) also demonstrated that selective predation of seedling macrophytes by snails could alter the final community developing from the propagule bank, thus highlighting a mechanism by which grazers could influence not just the abundance of plants but also their composition. Thus there is clear evidence that a top-down effect of fish on macrophyte growth can occur via a fish-macroinvertebrate-periphyton-macrophyte pathway, as first proposed by Brönmark and Weisner (1992). This mechanism complements the well-established planktonic trophic cascade via the fish-zooplankton-plankton-macrophyte pathway (Jeppesen et al., 1997). Thus we now know that both periphyton and phytoplankton provide a mechanism limiting light for macrophytes and that both can be influenced by top-down controls in addition to nutrients (Fig. 1).

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