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Submerged macrophyte decline in shallow lakes; what have we learnt in the last forty years?

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1 **1. Abstract**

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

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

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

14 The longer-term stability of macrophyte dominance is also reduced if there are few surviving plant
15 species. Such loss of species richness is associated with increased nitrogen loading. Submerged plants
16 also depend on a spring clear-water phase to become established, and local weather conditions during

17 winter and spring may determine the relative success of phytoplankton and plant growth, leading to a
18 progressively longer period of algal dominance and fewer surviving plant species.

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

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

26 **Key words:** shallow lakes, nutrients, alternative states, change, macrophyte ecology

27 **2. Introduction**

28 Forty years ago, ecological studies of shallow lakes intensified in response to the growing problems
29 arising from eutrophication. A particular concern at that time, at least in the UK, was the obvious loss of
30 submerged aquatic vegetation, its replacement by phytoplankton and the resulting loss of invertebrate
31 diversity (Morgan, 1970; Mason and Bryant, 1975; Phillips et al., 1978). Macrophyte loss is now clearly
32 recognised as being intimately linked with eutrophication, particularly in shallow lakes where the photic
33 zone extends over the majority of the bed, (Hargeby et al., 1994; Blindow et al., 2006) and many
34 attempts have been made to reverse this process (Moss, 1983; Moss et al., 1996a; Hilt et al., 2006;
35 Søndergaard et al., 2007). The success of lake restoration is often judged by how rapidly macrophytes
36 return, yet we still struggle to elucidate the ecological mechanisms for either the initial decline of
37 macrophytes or their frequently slow response to nutrient reduction (Lauridsen et al., 2003;
38 Søndergaard et al., 2007; Bakker et al., 2012).

39 It was early recognised that in very shallow lakes it might not be easy to account for macrophyte loss
40 simply through increased competition for light as a result of phytoplankton growth, and a model was
41 therefore proposed where increased periphyton growth initially suppressed plant growth, with
42 phytoplankton subsequently becoming dominant (Phillips et al., 1978). This hypothesis pre-dated the
43 idea of alternative equilibria that has become so important in understanding shallow lake systems
44 (Uhlmann, 1980; Irvine et al., 1989; Scheffer et al., 1993), but it was a perhaps an augury of the concept,
45 as it assigned macrophytes to a central stabilising role in the functioning of shallow lakes. What has
46 emerged over the last forty years is a clearer understanding of how macrophytes influence the ecology
47 of shallow lakes, in particular the positive feedback systems that maintain what are now widely
48 recognised as the alternative stable states of macrophyte-dominated clear water and plankton-
49 dominated turbid water (Jeppesen et al., 1998b; Burks et al., 2006).

50 When present, extensive macrophyte beds sequester nutrients (Blindow, 1992b; Ozimek et al., 1993;
51 Van-Donk et al., 1993; Kufel and Kufel, 2002), provide refuges from visual predators on grazing
52 zooplankton (Timms and Moss, 1984; Schriver et al., 1995), and may produce allelopathic exudates (Van
53 Donk and Van de Bund, 2002; Gross et al., 2007), all of which mitigate against phytoplankton growth
54 and thus maintain clear water conditions (Figure 1). Conversely, when macrophytes are absent, small
55 planktivorous fish reduce zooplankton grazing, and, free of the influence of visual predators in the
56 increasingly turbid water, can reach high densities thus promoting phytoplankton dominance (Jeppesen
57 et al., 1997). Numerous studies have demonstrated that these alternative states can exist over a
58 relatively wide range of nutrient conditions (Leah et al., 1980; Balls et al., 1989; Irvine et al., 1989;
59 Jeppesen et al., 2000; Jeppesen et al., 2003). Clear water and macrophyte-dominance conventionally
60 define the initial state of unimpacted shallow lakes, though whether this is truly a 'reference' state, or
61 merely one that reflects the shifting baseline effect of drift in perception, is a moot point. There are
62 indications that prior to expansion of human populations and depletion of large, nutrient-redistributing

63 grazing herds, some shallow lakes may naturally have been rich in nutrients and have had characteristics
64 that we would now see as detrimental (Moss, 2015). It is clear, nonetheless, that most become plankton
65 dominated under the pressure of nutrient addition, whether natural or artificial, while current aims of
66 conservation philosophy, which are perhaps more focused on issues of biodiversity than ecological
67 processes, are to maintain clear water with low-moderate nutrient concentrations in which a high
68 diversity and cover of macrophytes can thrive. In this review, we summarise what we have learnt over
69 the last 40 years about the mechanisms that overcome the apparent stability of this system to allow
70 phytoplankton to become dominant, and how this should influence our approach to restoration.

71 **3. Light availability and competition with algae**

72 While at a very broad geographic scale, the proportion of lakes dominated by submerged macrophytes
73 clearly decreases with increases in total phosphorus (TP) and total nitrogen (TN), logistic models
74 quantifying this relationship show wide variation, which can be linked, through climatic differences, to
75 the relative production of algal biomass and water depth, suggesting that light may still be a key issue
76 (Kosten et al., 2009). Early reports of macrophyte loss following eutrophication assumed this was a
77 consequence of reduced light availability caused by phytoplankton development (Mason and Bryant,
78 1975), as it had already been established by correlation that in deep lakes light was a key factor
79 influencing the depth distribution of macrophytes (Spence and Chrystal, 1970). This nutrient-
80 chlorophyll-light relationship remains true (Chambers and Kalff, 1985; Sand-Jensen and Madsen, 1991;
81 Middelboe and Markager, 1997), although the relationship between the maximum colonised depth of
82 macrophytes and nutrient concentrations is weak, not least because of the influence of coloured
83 dissolved organic substances and suspended inorganic matter, whose concentrations are largely
84 independent of nutrients. This suggests a more complex relationship linking nutrients to the distribution
85 and development of macrophytes (Søndergaard et al., 2013) and one which does not necessarily assume
86 that the loss of macrophytes is consequential on nutrient increase and phytoplankton development.

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

97 The relationship between nutrients and periphyton in lakes is, however, variable. Some studies
98 demonstrate an increase of periphyton with nutrients (Moss, 1976; Eminson and Phillips, 1978;
99 Cattaneo and Kalff, 1980; Eminson and Moss, 1980; Jones et al., 1999; Jones et al., 2000; Bécares et al.,
100 2007; Beresford and Jones, 2010) and a greater response than phytoplankton (Sand-Jensen and
101 Søndergaard, 1981). However, others only found an impact of nutrients when fish were present
102 (Mazumder et al., 1989) or no relationship (Lalonde and Downing, 1991; Lambert et al., 2008). Using
103 experimental ponds, Jones et al. (2002) found that periphyton abundance on the surface of plants was
104 controlled by the density of grazing invertebrates rather than nutrient load, confirming previous
105 experimental studies which have demonstrated the beneficial impact of snails on submerged
106 macrophyte growth via the removal of epiphytes (Brönmark, 1985; Underwood, 1991; Underwood et
107 al., 1992).

108 Predatory fish influence densities of benthic invertebrates in lakes (Brönmark et al., 1992; Diehl and
109 Kornijow, 1998), though probably not to the same extent that they influence populations of
110 zooplankters in the much less structured open water environment (e.g. compare Moss et al. (1998) and

111 Kornijów et al. (2016)). Experimental manipulation of fish has demonstrated that in enclosures devoid of
112 molluscivorous (e.g. *Lepomis microlophus*) or benthivorous (e.g. *Tinca tinca*) fish, invertebrate grazers
113 increased, reducing periphyton and increasing macrophyte biomass (Martin et al., 1992; Brönmark,
114 1994). Direct manipulation of invertebrate (snail) densities produces similar results (Underwood, 1991;
115 Underwood et al., 1992). Elger et al. (2009) also demonstrated that selective predation of seedling
116 macrophytes by snails could alter the final community developing from the propagule bank, thus
117 highlighting a mechanism by which grazers could influence not just the abundance of plants but also
118 their composition. Thus there is clear evidence that a top-down effect of fish on macrophyte growth can
119 occur via a fish-macroinvertebrate-periphyton-macrophyte pathway, as first proposed by Brönmark and
120 Weisner (1992). This mechanism complements the well-established planktonic trophic cascade via the
121 fish-zooplankton-plankton-macrophyte pathway (Jeppesen et al., 1997). Thus we now know that both
122 periphyton and phytoplankton provide a mechanism limiting light for macrophytes and that both can be
123 influenced by top-down controls in addition to nutrients (Figure 1).

124 **4. Relevance to alternative states hypothesis**

125 Light availability is clearly also important for periphytic algal growth, and as a result the relationship
126 between nutrients and periphyton can be complicated by the shading influence of phytoplankton
127 (Hansson, 1988; Bécares et al., 2007). In a survey of 13 Danish lakes, Liboriussen and Jeppesen (2006)
128 found that periphyton biomass on artificial substrata was unimodally related to TP, with a peak biomass
129 at intermediate concentrations ($60 - 200 \mu\text{g TP l}^{-1}$), being progressively nutrient limited at lower and
130 light limited at higher concentrations. These values are within the range of nutrients often associated
131 with a transition between alternative stable states in shallow lakes and suggests that high epiphytic algal
132 growth is most probable at intermediate nutrient concentrations unless controlled by grazers,
133 particularly snails, which are more efficient than other invertebrate grazers (Underwood et al., 1992).
134 Liboriussen et al. (2005), using mesocosms in clear and turbid water lakes, showed that both fish and

135 light availability affected the biomass of periphyton, with the strongest top-down control in clear water
136 lakes. Thus the stabilising influence of invertebrate grazing on macrophytes, via a benthic feedback loop,
137 may be potentially more important during eutrophication than during nutrient reduction. In addition,
138 density of plant-associated invertebrates is inevitably lower in lakes where macrophytes have been
139 absent for several years (Hargeby et al., 1994) and thus it may take some time for recolonisation of
140 appropriate invertebrate grazers to re-establish this mechanism, adding to the potential for instability in
141 lakes subject to nutrient reduction. Prolific growth of benthic algae has been observed in clear water
142 lakes following biomanipulation of the fish community (Stansfield et al., 1999); this might be due to the
143 absence of the normal invertebrate grazing control but a rapid population increase of invertebrate
144 grazers unchecked by fish predation could also produce a similar outcome owing to selective grazing on
145 young regenerating plants (Elger et al., 2009). In a survey of 17 plant-dominated shallow lakes in UK,
146 Jones and Sayer (2003) found supporting evidence for the importance of this mechanism, as submerged
147 plant biomass was shown to be unrelated to nutrient concentration or water transparency, but was
148 significantly related to periphyton biomass, which in turn was significantly related to number of grazing
149 invertebrates and fish density. Thus we now have experimental and survey evidence for a more
150 complex model of eutrophication in shallow lakes, whereby increasing nutrient levels increase the
151 *potential* for both epiphytic and planktonic algal growth, but the expression of this is controlled by
152 invertebrate grazers, which in turn are influenced by fish predation (Figure 1).

153 Quasi-stable states are maintained by a variety of buffer mechanisms (Moss et al., 1996a) and the
154 interaction of fish, grazing invertebrates and properties of the plants themselves reflect these. There is
155 still controversy as to whether nutrients alone can drive a switch from macrophytes to algal dominance.
156 This is usually assumed and a body of hysteresis theory has been built around this assumption, but there
157 is no definitive evidence for it. Where plants have declined at high nutrient levels, there have always
158 been confounding variables, such as ingress of trace organic substances from sewage effluents that

159 might have toxic effects on grazing invertebrates, particularly *Daphnia*. Where, in experimental systems,
160 such possibilities have been removed, addition of large amounts of nutrients has been associated with
161 increased plant growth, albeit sometimes with a redistribution of biomass from submerged to floating
162 species (McKee et al., 2002; Feuchtmayr et al., 2009). The hypothesis of alternative states originally
163 rested (Irvine et al., 1989) on the states being alternatives over broadly the same environmental
164 conditions, including nutrient status. There has been some drift in meaning of the term as research in
165 this area has become popular and this complicates the interpretations different investigators have
166 placed on their results. However, the concept of buffer mechanisms needing to be overcome by a switch
167 mechanism (Moss et al., 1996b) for states to change is still extant (Moss, 2007).

168 **5. The switch mechanisms**

169 Given that alternative clear and turbid states are possible, it seems probable that some external
170 pressure must occur to cause a switch between the two equilibria (Bender et al., 1984). In many cases,
171 the loss of plants is reported as a rapid change (Moss, 1983; Bales et al., 1993; Hargeby et al., 2007;
172 Tátrai et al., 2008; Randsalu-Wendrup et al., 2014) and to explain this we seek major events. There are
173 plenty of direct and indirect mechanisms that destroy plants at a local scale through mechanical,
174 chemical and grazing damage (Moss et al., 1996a), thus destroying directly the stabilising aquatic plant
175 community. However, others interfere with the stabilising feedback mechanisms, such as catastrophic
176 changes to fish populations. This could be a fish kill caused either by winter ice cover, where for example
177 the loss of piscivores results in an increase of planktivorous fish (Hall and Ehlinger, 1989; Isermann et al.,
178 2004), or summer depletion of oxygen removing planktivorous and benthivorous fish (Carvalho, 1994;
179 Jeppesen et al., 1998a). Such events do occur and undoubtedly can influence the survival of
180 macrophytes, but it is unlikely that they are sufficiently common to single-handedly account for the
181 widespread reported loss of macrophytes.

182 A more insidious and potentially general mechanism than fish kills would be the effect of pollutants
183 other than nutrients acting directly on the grazers. Examples have been suggested to explain the loss of
184 plants from the shallow lakes that constitute the Broads, a system of medieval man-made lakes and
185 wetlands in eastern England. Here palaeolimnological studies have demonstrated an association
186 between macrophyte loss and elevated levels of tributyltin (TBT), an organotin compound used since the
187 1960s as a biocide in antifouling paints which were widely applied to boats in these inland waters (Sayer
188 et al., 2006), and the pesticides DDT and dieldrin (Stansfield et al., 1989). These authors suggest that in
189 an environment of increased nutrient loading, which existed at the time, macrophyte decline may have
190 been precipitated by the loss of grazing invertebrates, both molluscs and zooplankton, caused by these
191 chemicals. Waste water treatment effluent is often the source of nutrients whose increase may
192 heighten the risk of a switch from plants to algae occurring, but it is rarely acknowledged that effluents
193 are much more complex chemically than simple nutrient solutions. They contain a very large range of
194 heavy metals, trace organics, and salts, including endocrine disruptors, other pharmaceuticals and vanity
195 products (Mills and Chichester, 2005) most of which have not been tested in circumstances where they
196 may cause subtle effects on growth of zooplankton and other invertebrates. This is a largely unexplored
197 area that merits further attention.

198 There is also a strong relationship between wildfowl biomass and macrophyte abundance (Wood et al.,
199 2012), with herbivorous wildfowl showing a positive relation to periods of clear water and high
200 macrophyte density (Hansson et al., 2010). Bird grazing has been reported to remove significant
201 proportions of annual macrophyte production (Mitchell, 1989; Lodge, 1991; Woollhead, 1994) and bird
202 grazing could be another destabilising influence on macrophyte dominance, having the added impact of
203 releasing nutrients into the water column. On the assumption that plant palatability and nutritional
204 quality will increase with productivity as plants invest proportionally more in growth than defence, and
205 tissue nutrient contents increase, per capita consumption by herbivores ought to increase with

206 productivity. Whether this translates to increased impacts of herbivores at higher productivity remains
207 unclear, although there is evidence to support this (Gayet et al., 2011; Bakker and Nolet, 2014).
208 However, the impact of birds has only been clearly shown using small exclosures in lakes where
209 macrophytes are recolonizing, or in experimental ponds (Lauridsen et al., 1993; Søndergaard et al.,
210 1996; Hilt, 2006). Coot (*Fulica atra*) and mute swan (*Cygnus olor*) are prolific macrophyte grazers but
211 using estimates of grazing rates, and abundance of macrophyte beds in Lake Krankesjön, Sweden
212 Hansson et al., (2010) showed that only 2.6% of macrophyte biomass was removed and similar
213 conclusions were reached for Botshol, a small shallow lake in Netherlands dominated by charophytes
214 (Rip et al., 2006). Moreover, grazing is likely to be most intense in the autumn when bird numbers reach
215 peaks but macrophytes are already senescing, though whether this opens up the possibility of impacts in
216 subsequent years is unclear. However, in urban lakes and bird reserves, where wildfowl densities may
217 be artificially high owing to supplementary feeding, there are usually no macrophytes and dense algal
218 growths or muddy water (B Moss personal observations). As with fish populations, effects of birds are
219 therefore likely to be density-dependent. The possibility that there are other higher trophic level
220 interactions with macrophytes mediated by diving duck such as tufted duck (*Aythya fuligula*), pochard
221 (*Aythya ferina*) or omnivorous species such as coot, has rarely been considered, although there is some
222 evidence that these species increase in numbers following fish removal and vegetation recovery and,
223 presumably, an increase in invertebrate prey density.

224 In some cases, grazing by semi-aquatic rodents, such as coypu (*Myocaster coypus*) or muskrat (*Ondatra*
225 *zibethicus*), may also be important. In the Broads, coypu escaped from fur farms and became endemic
226 from the 1950s until they were eradicated in the late 1980s. It had been assumed that their diet was
227 largely marginal emergent vegetation and they were therefore likely to have been primarily responsible
228 for loss of marginal reed swamp (Boorman & Fuller 1981), but there is significant evidence from the
229 southern US and Italy where coypu are also invasive that their diet can be dominated by submerged

230 vegetation (Wilsey et al., 1991; Prigioni et al., 2005) and studies of a captive coypu population at
231 Calthorpe Broad confirm the level of reliance on aquatic vegetation of invasive coypu in the UK (Gosling,
232 1974). Even low densities of a native aquatic rodent, the beaver, have been found to exert a significant
233 impact on deeper water swamp species such as *Schoenoplectus lacustris* in Scotland (Willby et al., 2014).
234 Such species are key architects of littoral zone complexity and their loss from the Broads, regardless of
235 cause, is likely to have precipitated the decline of a diverse aquatic flora of sheltered margins (Madgwick
236 et al., 2011). Given that the carrying capacity of beavers in Norfolk has been estimated at 18-40
237 territories (<200 animals) (South et al., 2001), while numbers of coypu in Norfolk may have been as high
238 as 20,000 in the mid 1970s (Gosling, 1974) it seems highly likely that coypu exerted an unsustainable
239 level of grazing pressure on littoral marginal vegetation and associated macrophytes. At their natural
240 carrying-capacity the effects of beavers on aquatic vegetation are likely to be sustainable, since animals
241 abandon territories after 5 years or so, moving to other sites, during which vegetation recovery in
242 former territories is likely. Elsewhere, large populations of grazing mammals and their predators also co-
243 exist with rich and abundant macrophyte populations, for example the capybara, jacaré and jaguar in
244 the Pantanal. There are dangers in attributing fundamental importance to the behaviour of introduced
245 species like coypu, without their predators, in situations that are far from natural, though with changing
246 climate and ongoing invasions such situations may increasingly become the norm.

247 Benthivorous fish can also influence macrophyte survival, through physical uprooting (Zambrano and
248 Hinojosa, 1999) and disturbance of sediment (Ibelings et al., 2007). In a survey of 28 lakes, Zambrano et
249 al. (2006) found that lakes with high benthivorous fish biomass were characterized by few macrophyte
250 species and it is the introduction of such fish that may precipitate macrophyte loss (Zambrano et al.,
251 2001). Plants were apparently lost as a result of fish stocking from a lake at Llandrindod Wells in mid-
252 Wales, which received extremely low-nutrient inflows. Common carp (*Cyprinus carpio*) were shown to
253 mobilize nutrients from the sediments in summer and large algal crops ensued (Moss et al., 2002).

254 Similarly, vigorous mechanical clearance (Balls et al, 1989) or excessive motorboat activity (Willby &
255 Eaton, 1996) and even the damage wrought by extreme storms, may act as switch mechanisms,
256 although the evidence tends to be anecdotal.

257 All of the above factors are possible mechanisms which could act as destabilizing influences. While they
258 are most often considered in isolation, the likely norm is that they operate in combinations that differ
259 between lakes, and will vary individually in their severity in response to climatic factors. Some are likely
260 to increase in importance with nutrient concentrations whilst others could potentially affect any lake,
261 though their impacts may be greater at higher nutrient concentrations.

262 6. **Rapid switches or gradual transitions?**

263 While the switch from clear to turbid water sometimes occurs relatively suddenly, historical records and
264 palaeolimnology on a decadal – centennial timescale show that there is often a more gradual shift, with
265 reducing macrophyte abundance and diversity rather than sudden loss (Sand-Jensen et al., 2000;
266 Davidson et al., 2005; Sayer et al., 2010a). Initially, there is a decline in small, slow-growing, rosette-
267 leaved species and charophytes (Blindow, 1992a; Sand-Jensen et al., 2000), and their replacement by a
268 more prolific growth of taller canopy-forming plants, such as *Ceratophyllum* and *Potamogeton* species,
269 in response to reduced light availability (Blindow, 1992a; Brodersen et al., 2001). This was demonstrated
270 experimentally in ponds in the USA (Moss, 1976) where charophytes predominated at low and medium
271 nutrient concentrations and *Elodea* at high concentrations but with reduced total biomass, attributed to
272 phytoplankton shading. In sheltered environments, the increase in water-column nutrients may also see
273 an increase in cover of free-floating macrophytes. So, while remaining macrophyte-dominated, water
274 clarity may reduce and with it the number or density of macrophyte species. For example, Sayer et al.
275 (2010a) demonstrated a reduction over time from 10 or more taxa to 4 in a small shallow alkaline lake,
276 resulting in a less structurally complex system. Analyses of large scale spatial (Willby et al., 2012) or long

277 term (Phillips et al., 2015) datasets reveal a similar pattern of change with plant richness declining
278 following a peak at low to moderate chlorophyll, TP or nitrate (James et al., 2005) concentrations. In
279 larger or slightly deeper lakes, macrophytes become restricted to shallower areas with less of the lake
280 containing significant macrophyte beds.

281 An additional development has been to discriminate between effects of nitrogen and phosphorus.
282 Meta-analyses of nutrient enrichment experiments by Elser et al. (2007) have shown that, for algal
283 growth at least, there are about as many instances of nitrogen limitation as of phosphorus limitation
284 and considerably more of co-limitation by both nitrogen and phosphorus. Species richness of submerged
285 macrophyte communities decreases with increasing winter nitrate concentrations (James et al., 2005)
286 and in mesocosm experiments with moderate phosphorus concentrations, growth and diversity of
287 submerged macrophyte communities declined with increasing nitrate loading (Barker et al., 2008). The
288 physiological basis for such effects is poorly understood, although Boedeltje et al., (2005), who,
289 experimentally, observed significantly reduced growth of *Potamogeton alpinus* at high nitrate
290 concentrations, speculate that nitrate-dominated N assimilation acts as a carbon and energy drain on
291 plants adapted to ammonia uptake. Macrophyte growth tends to be less strongly related to phosphorus
292 than that of phytoplankton (Lyche-Solheim et al., 2013), because macrophytes have access to
293 phosphorus sources in sediments that elude phytoplankton, which puts greater emphasis on nitrogen
294 supply for macrophytes than for planktonic algae. It is increasingly clear that the hegemony exercised
295 by phosphorus in thinking in this area is misplaced.

296 There have been different estimates of the proportions of lake area that are required to stabilise the
297 plant-dominated system; it could be as low as 10% (Søndergaard et al., 2010) or as high as 60% (Blindow
298 et al., 2002), perhaps depending on whether the main stabilising mechanism is via sheltering of
299 invertebrates (whether plant-associated or planktonic) or nutrient sequestration, but the end result of
300 reduced plant cover and diversity is a potentially less stable system. There is equal uncertainty about

301 timing of macrophyte growth. Few studies have investigated in detail the seasonal dynamics of
302 macrophyte growth, however, Sayer et al. (2010b) in a study of 39 shallow lakes in the UK and Denmark
303 were able to split lakes into three characteristic groups based on the seasonal abundance of plants in
304 June and August. “Turbid” lakes with few macrophytes, “stable” lakes where plants and clear water
305 were found in both seasons and “crashing” lakes where macrophytes were present in June but not in
306 August when their water became turbid. The “crashing” lakes with a short duration of macrophyte
307 cover were typically dominated by one or more of *Potamogeton pectinatus*, *Potamogeton pusillus* and
308 *Zanichellia palustris*, while those with a long duration of cover had a more diverse macrophyte
309 community. Sayer et al. (2010b) concede that from their study, it is impossible to separate cause from
310 effect. Is the short macrophyte growth-season a response to shading caused by phytoplankton or
311 possibly epiphyte development, or is it the plankton that take advantage of the temporary absence of
312 macrophytes? However, the species involved in the “crashing” lakes are typically associated with higher
313 nutrient concentrations (Kolada et al., 2014); they also die back in winter and may be adapted to a short
314 growing season. This contrasts with the long growth-period and frequent overwintering of charophytes.
315 A very similar set of changes was reported for Lake Müggelsee, in Germany, with the replacement of a
316 diverse charophyte-dominated flora by *P. pectinatus* and *Z. palustris* and high water transparency in
317 spring, but declining in mid-late summer (Hilt et al., 2013). Thus, as eutrophication progresses, it is
318 possible that the growing season of macrophytes becomes progressively shortened through increases in
319 summer phytoplankton. The boom-bust population dynamics of widespread invasive species, such as
320 *Elodea*, that tend to dominate in already species-poor eutrophic lakes in Europe may further promote
321 overall instability in plant cover and offer a window for phytoplankton establishment, though whether
322 invasion status affects switching behavior in lakes is presently unknown.

323 Where winter ice cover is frequent, as on the Boreal Plain of western Canada, macrophyte-dominated
324 systems are commonplace, and many lakes are fish-free (Bayley and Prather, 2003). However, using a

325 combination of remote sensing and ground survey covering a 20-year period, Bayley et al. (2007)
326 demonstrated that the majority of these lakes show relatively frequent changes between macrophyte
327 and plankton-dominated states. Most of the lakes in the region had concentrations of TP from 25– 100
328 $\mu\text{g l}^{-1}$, similar to the range of concentrations over which alternative states are likely to exist (Scheffer and
329 Jeppesen, 1998) and thus, being in a relatively pristine landscape, these lakes may illustrate the
330 mechanisms influencing the successful establishment of macrophytes (Bayley et al., 2007). Owing to the
331 severe winter, these lakes are “reset” each year, with both zooplankton and macrophytes having to re-
332 establish from eggs and propagules during the spring. Although the majority (70%) of the lakes in any
333 one year were clear, only 20% remained clear for the whole 20-year survey period; furthermore, of the
334 unstable lakes, on average 25% switched in synchrony. All of the lakes were very shallow and should
335 support substantial cover of submerged macrophytes; the fact that in some years they did not, suggests
336 that success of macrophytes was linked to conditions in the spring which could be influenced by local
337 weather, especially rainfall, and possibly the brownness of the water in this peaty landscape. Like the
338 crashing European lakes (Sayer et al., 2010b), these Canadian lakes are species poor (albeit in this case
339 naturally so), increasing the likelihood that adverse weather could have detrimental impacts. Thus, with
340 moderate nutrient levels, the establishment of one or two important species of macrophytes in
341 competition with phytoplankton can be envisaged as a lottery that is loaded according to the availability
342 of plant propagules, eggs of invertebrate grazers, timing of algal growth and local weather conditions.
343 Similar factors are commonly invoked to explain the failure of macrophytes to respond rapidly to
344 improved conditions in restored lakes.

345 There is also evidence of more frequent changes of state in European lakes. Lake Tåkern and Lake
346 Krankesjön in southern Sweden have switched four and three times respectively over the last five
347 decades (Hargeby et al., 2007). Both lakes have spent longer periods dominated by macrophytes than
348 by plankton, with turbid periods persisting on average for only five years, suggesting that the stabilising

349 forces in favour of macrophytes were relatively strong. In both cases the transition from turbid to clear
350 state was started by the establishment of the fast-growing canopy-forming macrophytes, *P. pectinatus*
351 or *Myriophyllum spicatum*, which were later replaced by charophytes, a reverse of the sequence of
352 change from clear to turbid where charophytes were replaced by angiosperms (Blindow, 1992b). There
353 is no clear explanation for these changes, but weather conditions were likely to have been involved. For
354 example, just prior to the most recent shift to turbid conditions in Lake Tåkern an unusually high spring
355 phytoplankton biomass occurred, potentially linked to high rainfall and greater input of nutrients
356 (Hargeby et al., 2007). High water levels in spring in the mid-1970s were also highlighted as a potential
357 explanation for a switch to turbid water (Blindow, 1992b) and low water to a switch back to
358 macrophytes (Blindow et al., 1993). In these lakes, changes in fish populations also took place, as a
359 result of winter fish kills and these are also likely to have influenced conditions. However, the transition
360 to a species-poor, canopy-forming plant assemblage, immediately before and after the switch in states,
361 and the possible influence of weather conditions influencing the light climate via water level changes
362 and plankton growth during the spring, give a very similar picture to that provided by Sayer et al.,
363 (2010a) of a species-poor macrophyte community being squeezed between spring and late summer
364 plankton blooms.

365 The spring clear water phase that occurs in eutrophic lakes (Lampert et al., 1986) is probably a key
366 window for submerged macrophyte establishment. Its existence results from grazing zooplankton and
367 its length and timing can be dependent on weather conditions during the winter and spring, which
368 influence both grazing zooplankton numbers (de Senerpont Domis et al., 2007) and the migratory
369 movement of planktivorous fish as they seek to minimise their own risk of predation by moving out of
370 lakes to tributary streams during winter (Brönmark et al., 2010). The timing and proportion of fish
371 migrating varies between years and can be linked to fish condition, food availability and potentially local
372 climate. Brönmark et al. (2010) offer a speculative model which links clear-water, macrophyte-

373 dominated systems to better fish condition, higher winter migration, greater zooplankton survival and a
374 re-enforcement of the spring clear water period, with the opposite true for turbid states. Given the
375 potential for weather to influence these seasonal events and the reliance of canopy-forming
376 macrophyte taxa on regrowth from overwintering propagules (Van den Berg et al., 1999), there is clear
377 potential for a loss of synchrony, potentially driving an already macrophyte-species poor and therefore
378 unstable lake to phytoplankton-dominance. Availability of light for macrophytes is also influenced by
379 water level and several studies have reported stronger growth of macrophytes when water levels were
380 low (Beklioglu et al., 2006; Bucak et al., 2012; Ejankowski and Solis, 2015). Water level changes,
381 themselves potentially linked to rainfall, or lake management, are thus an additional factor that could
382 control macrophyte development during the spring.

383 There are also indications of regular cyclical growth of macrophytes with a periodicity of 5-7 years (Moss
384 et al., 1990; Blindow et al., 1993; Perrow et al., 1994; Rip et al., 2005). It has been suggested that these
385 changes are linked to the storage and subsequent release of phosphorus due to buildup of organic
386 matter in the sediment which subsequently influences the summer release of phosphorus (Genkai-Kato
387 and Carpenter, 2005; Van Nes et al., 2007) and hence the development of phytoplankton. However, it
388 has been shown that the TP cycle found in Botshol (Rip et al., 2005) can also be accounted for by rainfall
389 patterns (Rip et al., 2007). Hargeby et al., (2006) also noted that the total organic nitrogen concentration
390 in Lake Tåkern oscillated with a periodicity of 8 years during the clear water, macrophyte-dominated
391 period and that this could be cross-correlated to the North Atlantic oscillation (NAO) which might
392 therefore be linked to macrophyte production, although no causative mechanism was identified. In a
393 review of long-term data on macrophyte abundance in several shallow lakes in the Norfolk Broadland,
394 Phillips et al. (2015) noted that lakes more isolated from the rivers, with recovering, (at least
395 temporarily), but species-poor macrophyte communities showed long-term synchronous cycles
396 suggestive of weather-related influences, with peak abundance occurring in warm sunny years. Thus

397 there is growing evidence that local weather events can influence the development of macrophytes and
398 the outcome of their competition with algae for light. While this is undoubtedly not a new phenomenon
399 climate change and increased inter-annual variability in weather conditions are likely to raise its
400 importance.

401 **7. Conclusions**

402 Over the last 40 years it has become clear that, when present, macrophytes have a competitive
403 advantage over algae. To that extent the original graphical conceptual model of Phillips et.al, (1978)
404 remains valid. What it did not include were the feedback mechanisms of the grazers and the potential
405 instability that this creates (Figure 1). Provided the macrophyte associated invertebrate grazing fauna,
406 both planktonic and benthic, are intact, this advantage is largely independent of nutrient load. In
407 shallower lakes, macrophytes can occupy a large proportion of the lake basin and, if evergreen taxa such
408 as charophytes dominate, can lock up, at least temporarily, substantial proportions of a lake's
409 phosphorus. However, with increasing nutrient loads the integrity of this system is sensitive to a wide
410 range of stochastic events, many perhaps driven by local weather conditions, which create a window of
411 opportunity for algal growth. The resultant increase in shading filters the macrophyte species pool until
412 only fast-growing canopy-forming or free-floating species persist (Kolada et al., 2014). These remaining
413 macrophytes also become compressed within a seasonally defined "sandwich" (Sayer et al., 2010a) and
414 are ultimately replaced by plankton. The loss of macrophytes from lakes might be better perceived as
415 the gradual erosion of a competitive advantage rather than a sudden switch in state, but with increased
416 nutrient loading it seems inevitable that events will sooner or later conspire to accelerate this loss.
417 Recovery of macrophytes may subsequently be engineered but all the evidence suggests that sustained
418 recovery requires significant reduction in nutrient concentrations (Jeppesen et al., 2012).

419 Lakes have traditionally been managed as discrete entities with only intellectual cognizance given to the
420 reality that the unit of management is the catchment. This approach has a long tradition in European
421 conservation and still determines attitudes to terrestrial conservation. It has meant however, that lakes
422 have been seen in isolation, as closed systems and with equilibrium communities that can be managed
423 by suitable manipulation. Such quasi-equilibria may last for some time, perhaps as long as a couple of
424 scientist-career spans, but our increasing understanding is that lakes are very open systems that have
425 always been continually changing in response to natural climatic fluctuations and geological events.
426 Phases of apparent stability in dynamic systems will always prove beguiling and may attract a value if
427 attributes such as aesthetics, rarity or diversity appeal in the context of that period of history. But this
428 value is notional and has little relevance to the long-term march of natural processes. Phillips et al.
429 (1978) began a process of understanding the mechanisms that influence lake state that morphed into a
430 general consideration of particular states and how they were maintained. There are some examples that
431 might fit their original hypothesis and they are of great intellectual interest. But they may cloud a
432 greater picture of change that can be slow or rapid, extensive or subtle and in which simple patterns and
433 hypotheses do not apply. The intense influence of ourselves has made it very difficult to interpret
434 change because changes come in many forms and are sometimes not easily recognized, especially at
435 first, against a background of short-term natural variation, and their causes even less readily diagnosed.
436 Monitoring change where there are no unchanging controls, if any control at all, will always struggle to
437 reveal mechanisms objectively. Experiments can reveal mechanisms but the specific experimental
438 circumstances may capture merely a snapshot of a lake's history. Nonetheless a degree of
439 understanding has been revealed using replicated experimental mesocosms that allow hypothesis-
440 testing, alongside analysis of sediment cores to determine change in a range of chemicals and sub-fossils
441 over centuries, and potentially millennia, though such perspectives have only recently begun to figure in
442 lake management (Sayer et al., 2012). We have used large scale surveys which depend on space-for-

443 time substitution and finally a small number of long-term monitoring programmes. All individually have
444 strengths and weaknesses, but in combination they have delivered an understanding of shallow lakes
445 and the central role that submerged macrophytes play in their ecology. It is the diversity of the positive
446 feedback pathways that macrophytes provide, and the different time scales and evolving background
447 against which these operate (Scheffer and van Nes, 2007) that make it impossible to provide a simple
448 all-encompassing mechanistic model relating macrophyte loss to eutrophication. Given that
449 eutrophication itself represents a syndrome of co-occurring pressures, such simplicity must always be
450 questioned.

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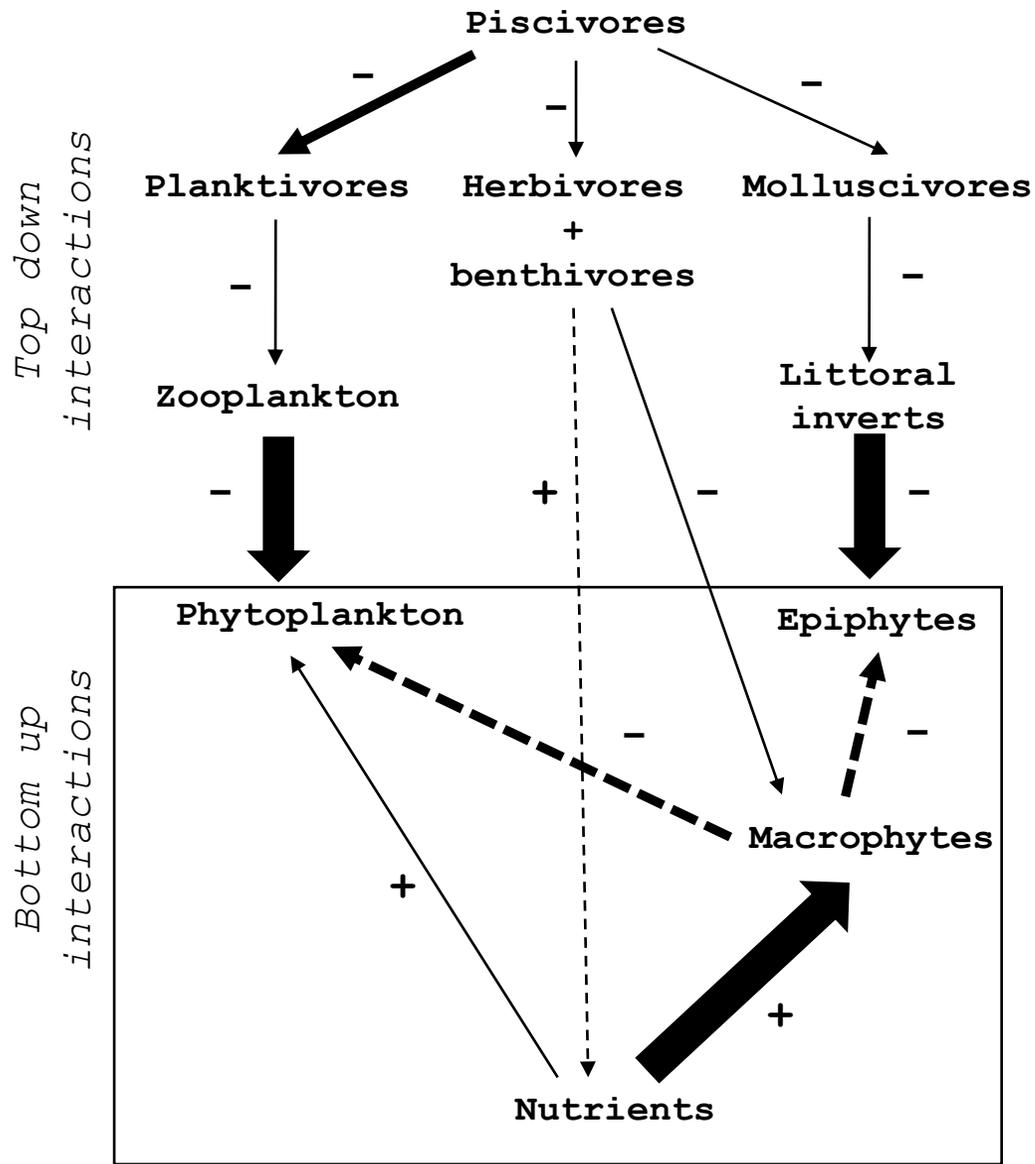
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Figure caption: Major interactions in shallow lake ecosystems. The left hand diagram summarises interactions in clear water, macrophyte-dominated lakes, the right hand diagram shows interactions in turbid-water algal-dominated lakes. Pressures on different ecosystem components that may trigger a sudden or gradual shift to algal dominance are shown in the central column. In addition to these pressures interannual variation in water temperature, water depth and sunshine hours will strengthen or weaken particular interactions by affecting, for example, year class strength in fish, hatching dates in zooplankton and the onset of growth in macrophytes. Symbols show the direction of the effect and arrows show the magnitude of the effect. The bottom half of each diagram focuses on bottom up effects related to nutrients. The top half of each diagram shows top-down effects. Dashed arrows show other effects including allelopathy, nutrient sequestering, shading, bioturbation and physiological constraints. The original model of Phillips et al. (1978) dealt with interactions shown within the bottom-up compartment. For simplicity feedback effects of macrophytes on piscivores and littoral invertebrates via provision of refugia are not shown. Note that in some lakes the piscivore, herbivore and molluscivore components will relate to both fish and waterbirds.

Figure

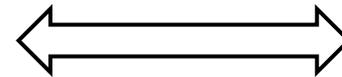
Clear water, macrophyte dominated



Key pressures

Habitat loss, DO and ice-induced fish kills

Habitat loss, agrochemicals, other toxins, salinity



Non-native grazers, boating, weed-cutting, invasion, toxins, salinity, water level rise

Internal loading, increased external load

Turbid water, algae-dominated

