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1 **Modelling lake phytoplankton communities: recent applications of the PROTECH**
2 **model**

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23 **Abstract**

24 Understanding and modelling the development of lake phytoplankton communities is a
25 desirable goal, given the importance of these organisms to their ecosystem. PROTECH
26 (Phytoplankton **Resp**Onses **T**o **E**nvironmental **CH**ange) is one such model which attempts to
27 do this and its applications over the last 10 years are reviewed here. These studies include:
28 modelling very large lakes, linking catchment models to PROTECH, simulating oxygen
29 concentrations, understanding the importance of nutrient source in moderating the influence
30 of hydraulic retention time. Furthermore, the merits of ensemble lake modelling are
31 considered, as are the limits of short term forecasting of blooms. Finally, climate change
32 influences are examined with studies that include nutrient changes and an experiment that
33 attempts to separate the influences of temperature and mixed depth.

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37 **Introduction**

38 Understanding the responses of ecosystems to drivers lies at the heart of most ecological
39 research. Through quantification of the environment, mathematical relationships can
40 sometimes be found which describe these responses leading to the possibility for prediction
41 and modelling. This quantification can be derived from observational field data or
42 experiments and it was the latter that Colin Reynolds used in the 1980s to explore the nature
43 of phytoplankton growth rates.

44 Reynolds (1989), through a series of laboratory experiments under idealised
45 conditions, found relationships between the growth rates of a range of different lake
46 phytoplankton species and their morphology. Thus, if the surface area, volume and
47 maximum linear dimension of a species was known, the response of its growth rate to
48 changes in temperature and light availability could be estimated using equations derived from
49 Reynolds' experiments.

50 Following this work, Reynolds went on to begin the construction of a computer model
51 with a colleague, Anthony Irish. At its heart lies the equations of Reynolds (1989) but further
52 enumeration was required to allow for the effects of nutrient limitation upon growth rates and
53 various loss processes such as zooplankton grazing, sedimentation and flushing removal.
54 With the final addition of species-specific daily vertical movements, the biological core of the
55 new PROTECH (**Phytoplankton RespOnses To Environmental CHange**) model was
56 complete. The conception, equations and first 10 years of research of the PROTECH model
57 was extensively reviewed in Elliott et al. (2010), but this review will consider the new
58 PROTECH research from the last 10 years after a brief overview of the model.

59

60 **The PROTECH model**

61 PROTECH is a 1D-lake phytoplankton community model that works in daily time steps. The
62 spatial structure is constructed using bathymetry data describing the changing surface area
63 and volume. This creates a series of vertical layers in the model, each 0.1 m deep. The
64 physical thermal profile can be either calculated based on daily meteorological inputs (air
65 temperature, wind speed and air humidity) and inflow water temperature or it can be read in
66 from observed data or another model. A further physical consideration is to model water
67 exchange in the lake through inflow and outflow discharge. In PROTECH, it is assumed the
68 water entering the lake mixes with the surface mixed layer and the water leaving the lake also
69 comes from this layer unless it is a reservoir system where water is abstracted at depth.

70 The biological component is primarily focused on the phytoplankton community. The
71 individual phytoplankton are characterised by their morphology, daily movement,
72 vulnerability to grazing and nutrient requirements to reflect nitrogen-fixation and diatoms
73 (Table 1). The morphology information is used by the equations from Reynolds (1989) to
74 create phytoplankton specific potential growth rates for each depth layer in the model,
75 responding to changing temperature and light availability. The availability of nutrients to
76 support this growth is checked using specific thresholds (3, 80, 500 mg m⁻³ for phosphorus,
77 nitrate and silica respectively) and the growth rate reduced proportionally if any nutrients are
78 limiting.

79 Phytoplankton biomass loss is caused by filtration-based zooplankton grazing (the
80 phytoplankton maximum dimension must be < 50 µm, although there can be exceptions
81 based on natural observations), sedimentation out of the water column and dilution wash-out
82 caused by water exchange. Thus, after balancing the growth with the losses, a daily net gain
83 in biomass can be calculated for each layer in the model. Clearly, the model is more detailed
84 than this brief overview suggests and for further information it is recommended to consult
85 Elliott *et al.* (2010). Finally, at the time of the Elliott *et al.* (2010) review, PROTECH had

86 been applied in the peer-reviewed literature to ten water bodies, predominately in the UK
87 (Table 2). However, since then the model has been used in many more new studies (Table 2),
88 which are considered in this review.

89

90 **Applying PROTECH to large lakes**

91 Pre-2010, PROTECH had mainly been applied to relatively small lakes with the exception of
92 Lake Erken, Sweden (24 km²; Elliott *et al.*, 2007). However, since then it has been applied to
93 the UK's largest lake, Lough Neagh (383 km²; Elliott *et al.*, 2016), Pyhäjärvi in Finland (154
94 km²; Pätynen *et al.*, 2014) and Lake Simcoe, Canada (2899 km²; Crossman & Elliott, 2018;
95 Crossman *et al.*, 2019). Given the model's 1D nature, these studies were a new challenge and
96 for the first two studies, yet PROTECH performed satisfactory with only one modification
97 regarding sediment nutrient release, which is discussed below. However, for the very large
98 Lake Simcoe, the lake had to be divided into three separate basins where two side arms fed
99 into the large main basin and this approach worked well with the outflows from the separate
100 side arm simulations becoming inflows into the main basin simulation. It is amusing to note
101 that these two "side arms" were individually a similar size to England's largest lake,
102 Windermere!

103 Furthermore, these studies highlighted a weakness in PROTECH regarding the
104 model's lack of functions to elucidate nutrient release from sediments. In such large surface
105 area water bodies, sediment inputs can be an important source of nutrients, particularly
106 phosphorus, and from the three lakes discussed above a forced input of phosphorus had to be
107 added to the model using observed in-water nutrient data as a guide. Some other lake models
108 do include such functions (e.g. PCLake (Janse, 1997)) and it is something that will hopefully
109 be added to PROTECH in the future. However, one of the problems is that such a function

110 would require knowledge of nutrient sediment concentrations, something that is rarely
111 measured in standard programs of lake monitoring. This lack of data has certainly been the
112 case in many previous PROTECH studies, hence the forced introduction of nutrients to the
113 water column using in-lake measurements of nutrients.

114

115 **Linking the catchment to the lake through modelling**

116 Lakes are intrinsically part of their catchment and are affected by the types of land that make
117 up that area. Given this connection, it is understandable that the management of catchments
118 is a prevalent method for reducing nutrient inputs to lakes and thus improve their trophic
119 status. It also follows that using models that can adequately describe this connection are very
120 useful in exploring how changes in land use might impact upon the lake phytoplankton.

121 An example of such a cascade of different models is Norton et al.'s (2012) study of
122 Loweswater, UK, where a catchment model's (GWLF; Schneidermann et al., 2002) output
123 was used to drive PROTECH. Loweswater was suffering from poor water quality and
124 cyanobacteria blooms due to high nutrient inputs from the surrounding farm land. The
125 investigation tested the relationship between these nutrient inputs and the phytoplankton
126 produced by the lake through the application of a number of different land use scenarios.
127 These covered different ratios of livestock (cattle and sheep) as well as more extreme
128 scenarios such as no livestock with all grassland or all woodland.

129 The wide range of phosphorus loads created by the GWLF model and these nutrient
130 outputs were used to drive PROTECH. The resultant outputs from the two models allowed
131 the relationship between nutrient load and the modelled phytoplankton community to be
132 described (Figure 1). This was interesting because it showed that PROTECH produced two
133 different responses to the changing phosphorus loads. For example, the annual mean

134 chlorophyll produced by PROTECH grew with increasing loads producing an asymptotic-like
135 curve whereas the increase in the cyanobacteria part of the community was linear (Figure 1).
136 Thus, the study suggested there was an escalating trend cyanobacteria dominance within the
137 community with increasing input nutrient load, despite a declining rate in production of
138 overall biomass.

139

140

141 **Modelling oxygen concentrations in PROTECH**

142 Oxygen was not a variable originally considered in PROTECH, so in a study that wished to
143 simulate the potential impact of climate change on the Vendace (*Coregonus albula* (L.)) fish
144 species, the Lake OXYgen model (LOX; Bell et al., 2006) was added into PROTECH (Elliott
145 & Bell, 2011). LOX works by dividing the vertical component of the lake into two layers
146 (epilimnion and hypolimnion) and its equations were used to create a new sub-routine in
147 PROTECH. By using PROTECH's temperature and chlorophyll data, LOX can estimate the
148 dissolved oxygen concentrations in the two layers and through a simple depth function create
149 an oxygen profile from the surface to the bottom of the lake.

150 If the approach of other lake models is considered, LOX's complexity is comparable
151 to PCLake's oxygen calculations (Janse, 1997), but is simplistic compared to DYRESM-
152 CAEDM (Hamilton & Schladow, 1997), which uses process-based calculation throughout all
153 of its layers, Nevertheless, LOX proved effective both for the Vendace study in
154 Bassenthwaite Lake, UK ($R^2 > 0.7$ against fortnightly observed O_2 ; Elliott & Bell, 2011) and
155 for the Lake Simcoe, Canada, study ($R^2 > 0.8$ against monthly mean observed O_2 ; Crossman
156 & Elliott, 2018) where the impacts of catchment land use changes on the lake's oxygen
157 concentrations were simulated.

158

159 **The effect of changes in hydraulic retention time**

160 Building upon previous PROTECH studies (Elliott et al., 2009; Elliott, 2010), further work
161 explored the importance of changing hydraulic retention time upon phytoplankton. Many
162 aspects of weather are predicted to change in the future and in a study focused on the
163 eutrophic Loch Leven, UK, PROTECH was used to assess the relative importance of
164 increasing water temperature and changing retention time (Elliott & Defew, 2012). The
165 study showed clearly that changes in inflow, both increase and decreases, were of greater
166 importance than temperature increase as large as 4 °C. In general, increased inflows which
167 caused a reduction in retention time were detrimental to the slower growing species in the
168 model leading to the heightened presence of smaller, faster growing phytoplankton.
169 However, this flow effect had a seasonal aspect to it because at times of year with naturally
170 low flows (e.g. summer), an increase actually benefited the phytoplankton by providing more
171 nutrients at a time when they were limiting growth. This was because the source of nutrients
172 to the lake were assumed to be diffuse leading to an increase in flow delivering a greater
173 nutrient load to the lake.

174 This importance of nutrient source was explored further in a PROTECH study of
175 Bassenthwaite Lake, UK (Jones et al., 2011). This model experiment recognised the
176 relationship between nutrient load to a lake and the type of nutrient source. Specifically, this
177 means a load derived from a point nutrient source is independent of the flow whereas a
178 diffuse source load changes in proportion with inflow. To test the importance of source, 32-
179 year flow scenarios were run based on a number of climate change scenarios. These runs
180 provided a large range of retention times over which annual and seasonal means could be
181 calculated.

182 The results showed that the sensitivity of nutrient source to changes in flow was
183 seasonally dependent: winter and autumn were the least responsive with spring and summer
184 being the most sensitive. Furthermore, for the sensitive seasons, the nature of the relationship
185 was greatly dependent upon nutrient source. Thus, for the flow-independent scenarios short
186 retention times produced less phytoplankton biomass than when retention time was long
187 (Figure 2). Conversely, with flow dependence, high inflows increased biomass and low
188 flows saw little decline in chlorophyll (Figure 2). The mechanism behind these differences
189 was the balance between the dilution loss of biomass caused by high flows and the potential
190 to bring more nutrients into the lake and thus stimulate more phytoplankton growth.
191 Therefore, whilst the former is a universal effect with high flows, the latter can only happen
192 under the flow-dependent (diffuse) conditions.

193

194 **Ensemble modelling**

195 Uncertainty in model parameters and construction is a constant issue. An approach used in
196 other disciplines (e.g. weather forecasting) is to apply different versions of the same model
197 (the most common approach) or different models (much rarer) to the same scenarios and then
198 amalgamate the results to provide a predicted mean and uncertainty envelope. In ecology,
199 though, it is a method that seems to be rarely used therefore, in Trolle et al. (2014) an
200 ensemble of different lake models was applied to Lake Engelsholm, Denmark.

201 Three lake models formed the ensemble: DYRESM-CAEDYM (Hamilton &
202 Schladow, 1997), PCLake (Janse, 1997) and PROTECH. It should be noted that this
203 approach of using independently created models for the ensemble is rare and clearly has a
204 greater capability of capturing more levels of uncertainty than would be gained from simply
205 using re-parametrisations of one model. For calibration and validation, a three-year

206 simulation was conducted and model performance at the daily and monthly level was
207 assessed using observation data to determine the coefficient of determination (r^2) and relative
208 absolute error. These statistics showed clearly that the mean values created from the three
209 individual models' outputs was a better fit to the observations than any individual model
210 managed to produce. Coupled with that, the combination of the models also produced an
211 uncertainty range using the minimum and maximum values from the models. This showed
212 that the greatest area of uncertainty was during the summer where phytoplankton biomass
213 was at its highest. Using this baseline, a number of climate change scenarios were then run
214 for the lake and showed that small increases in water temperature increased both the total
215 phytoplankton and cyanobacteria biomass.

216

217 **Forecasting phytoplankton abundance**

218 Being able to forecast phytoplankton abundance in a way similar to weather forecasts is a
219 challenging goal but it was attempted recently using PROTECH. This ambitious programme
220 of research had two phases, the first being to test and understand the behaviours of
221 PROTECH when driven by high frequency in-lake observations (Page et al., 2017). This was
222 done using sub-daily buoy data collected from three lakes in the English Lake District
223 (Blelham Tran, Esthwaite Water and Windermere). The results revealed that the most
224 difficult aspect of forecasting was not the future weather uncertainty but rather the
225 uncertainty surrounding the daily nutrient load to the lake.

226 Building upon this initial testing, a second phase of modelling used historic weather
227 forecasts that used an ensemble of 50 simulations of 10-days-ahead weather to drive the
228 model coupled with stochastic perturbations of model parameters (Page et al., 2018). This
229 allowed PROTECH, day by day, to forecast a range of possible futures and create an

230 uncertainty envelope. Windermere and Esthwaite Water were used for these tests and the
231 results were compared to the benchmark prediction of persistence i.e. the chlorophyll
232 concentration will not change over the 10-day forecast period and is reset to equal new
233 observation data when they become available every two weeks. Given this criteria,
234 PROTECH was only better than the persistence forecast at a forecast range of less than six
235 days. In terms of the cyanobacteria forecast, the model was not successful of predicting its
236 biomass, showing the limitations of the approach at predicting specific species although it
237 was more successful at predicting functional types i.e. low-light or low-nutrient specialists.

238

239 **Climate change and nutrient load impacts**

240 Building on previous PROTECH investigations (Elliott et al., 2006; Elliott & May, 2008),
241 two additional studies were conducted examining the combined impact changing temperature
242 and nutrient load. These studies explored lakes that were different to the previous studies,
243 specially a larger lake (Windermere, UK) and a deep lake with a small surface area
244 (Rostherne Mere, UK).

245 Windermere is England's largest lake (64 m deep, 14.7 km² surface area) and has
246 been a focal point for tourism in the English Lake District for over 100 years (McGowan et
247 al., 2012). Correspondingly, the lake has been under ever-growing anthropological pressure
248 both in terms of its usage and ecosystem health. How those pressures would affect
249 Windermere in the future was the subject of a PROTECH investigation where water
250 temperature and nutrient load were altered in a factorial modelling experiment (Elliott, 2012).

251 Assessing the impact of these changes, it was clear that the simulated spring diatom
252 bloom was more influenced by the changes in temperature than nutrients, showing earlier
253 bloom peaks with increasing temperature. However, in the summer period increasing

254 nutrient load and water temperature synergised to enhance cyanobacteria growth. This led to
255 more days of exceedance of the World Health Organisation's cyanobacteria threshold of 10
256 mg m⁻³, but nutrients were the crucial factor with the reduced nutrient scenarios greatly
257 limiting the temperature impacts.

258 Rostherne Mere is a very different lake to Windermere with a depth of 31 m but only
259 a surface area of 0.49 km² (Radbourne et al., 2019). This basin shape leads to it having a
260 long, stable period of stratification lasting 9-10 months and to a depth of 10 m. Historically,
261 the lake has suffered from eutrophication driven by external nutrient sources, which led to the
262 diversion upstream of sewage effluent in 1991. However, due to the strong stratification in
263 the lake and corresponding sediment nutrient release, recovery has been very slow (Moss et
264 al., 2005). Therefore, to explore the potential future trajectories of recovery for Rostherne
265 Mere, the PROTECH model was applied (Radbourne et al., 2019).

266 The study used future climate scenarios from the UKCP09 projections (Murphy et al.,
267 2009) and coupled them with a range of external and internal nutrient scenarios. The results
268 reinforced the importance of the internal nutrient problem, quantifying that substantial
269 reductions in this source for decades would be needed to see improvements in the lake.
270 However, the scenarios towards the end of 21st century actually showed a reduction in
271 phytoplankton biomass because, with an increase in stratification length, the reliance by
272 phytoplankton upon external nutrients increased and given that this source had been reduced,
273 late summer biomass declined. Nevertheless, the winter overturn of the water column still
274 brought the considerable amounts hypolimnion nutrients to the surface, meaning that long-
275 term recovery was still hindered.

276

277 **Disentangling mixed depth and temperature effects**

278 The thermal structure of a lake varies annually in temperate regions with the formation and
279 dissipation of stratification occurring in many lakes. Physically, temperature and mixed layer
280 depth vary together as both variables can influence each other. However, changes in
281 temperature and mixed depth effect phytoplankton communities in different ways with the
282 former influencing cell metabolic processes and the latter effecting light and nutrient
283 availability. Given this correlation between temperature and mixing, it is very difficult to
284 attribute cause and relative importance to any observed changes in the lake phytoplankton.

285 Therefore, a PROTECH experiment on Blelham Tarn, UK, was conducted to separate
286 these relative effects by forcing the modelled lake structure (Gray et al., 2019). Essentially,
287 this meant artificially manipulating the mixed depth in the model independently of changing
288 the temperature and *vice versa*. Whilst such a thing would be highly unlikely in the real
289 world, it did allow great insight into the relative importance of changes in mixing and
290 temperature. For example, whilst stratification length was prevented from changing in the
291 model scenarios, increasing temperature alone caused an earlier spring bloom by accelerating
292 growth rates in the phytoplankton. Given such advances in bloom timing have been observed
293 in lakes (e.g. Thackeray et al., 2010), this model experiment shows that although changes in
294 stratification can be a cause of such advancement, temperature alone is capable of producing
295 the same effect.

296 Another emergent model result concerned cyanobacteria blooms in the summer and
297 autumn periods. Here, two different types of cyanobacteria dominated with different mixed
298 depths as temperature increased. Thus, the *Dolichospermum*-type in PROTECH thrived with
299 shallow mixing whilst the *Planktothrix*-type dominated with deep mixing. This suggested that
300 a shallowing of mixed depth in lakes where mixing is not too deep (e.g. < 5 m) would see
301 greater blooms of buoyant cyanobacteria. Conversely, lakes that currently experience blooms

302 of low-light tolerant phytoplankton, like *Planktothrix*, might see a decline in their dominance
303 if the deeper mixing (e.g. > 10 m) seen in those lakes shallowed in the future.

304

305 **The legacy of Colin Reynolds: PROTECH**

306 This review forms part of a special issue celebrating the legacy of Colin Reynolds who sadly
307 passed away in December 2018. That legacy includes PROTECH, a model which Colin was
308 so fundamental in conceiving and creating. When I was lucky enough to fall under Colin's
309 mentorship and begin to use PROTECH, we used to joke that the model was a digitization of
310 his brain, taking his great knowledge of phytoplankton and turning it into the "0s and 1s"
311 binary of the computing world!

312 Of course, since those early days, PROTECH has continued to be applied to lakes all
313 around the world, flourishing and developing to face new challenges and creating a growing
314 body of research, the latest of which has been reviewed here. I have no doubt that in the
315 future PROTECH will continue to contribute to our understanding of lakes and their
316 phytoplankton, and that through such work, an important part of Colin's legacy will live on.

317 Finally, I would like to record here my heartfelt thanks to Colin for all the support he
318 gave me over the years: he was a great mentor, colleague and, perhaps most importantly,
319 friend. You are missed by me, every day.

320

321

322 Table 1. Some examples of the information used by the model to simulated a given
 323 phytoplankton.

Name:	<i>Chlorella</i>	<i>Asterionella</i>	<i>Dolichospermum</i>
Maximum Dimension μm	4	130	75
Surface Area μm^2	50	6690	6200
Cell Volume μm^3	33	5160	29000
Grazed:	True	True	False
Diatom:	False	True	False
Nitrogen fixer:	False	False	True
Move per day:	Down 0.1 m	Down 0.2 m	Light condition ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$): >100 = Down 0.3 m >30 = Down 0.1 m <30 but >10 = No move <10 = Up 0.1 m

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336 Table 2. List of lakes and reservoirs where PROTECH has been applied and tested in peer-
 337 reviewed studies. Studies post-2010, considered in this review, are highlighted in **bold**.

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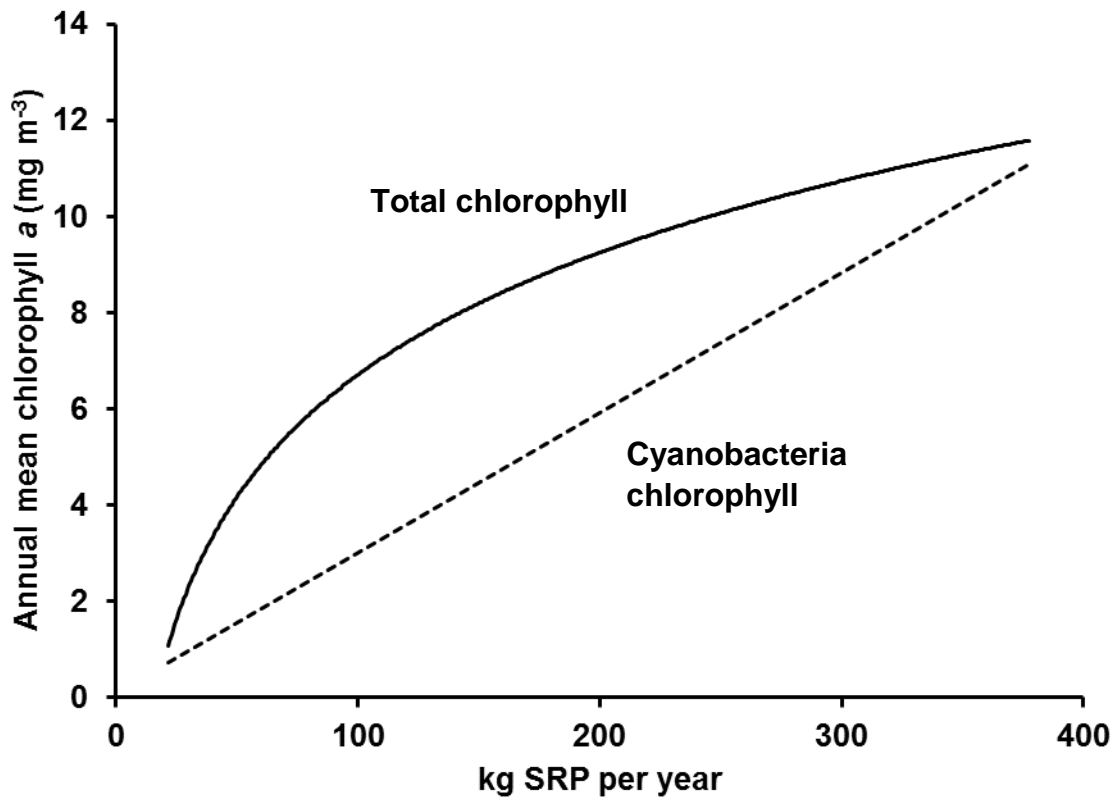
Water body (Country)	Trophic status	Reference
Bassenthwaite Lake (UK)	Mesotrophic/Eutrophic	Elliott et al., 2006; Bernhardt et al., 2008
Blelham Tarn (UK)	Eutrophic	Elliott et al., 2000; Gray et al., 2019
El Gergal Reservoir (Spain)	Eutrophic	Elliott et al., 2005
Lake Engelsholm (Denmark)	Eutrophic	Trolle et al., 2014
Esthwaite Water (UK)	Eutrophic	Elliott, 2010
Lake Erken (Sweden)	Mesotrophic	Elliott et al., 2007
Farmoor Reservoir (UK)	Mesotrophic/Eutrophic	Hutchins et al., 2018
Loch Leven (UK)	Mesotrophic/Eutrophic	Elliott & May, 2008; Elliott & Defew, 2012
Loweswater (UK)	Eutrophic	Norton et al., 2012
Myponga Reservoir (Australia)	Eutrophic	Lewis et al., 2002
Lough Neagh (UK)	Eutrophic	Elliott et al., 2016
Pyhäjärvi (Finland)	Mesotrophic/Eutrophic	Pätynen et al., 2014
QE II Reservoir (UK)	Eutrophic	Reynolds et al., 2005
Rostherne Mere (UK)	Eutrophic	Radbourne et al., 2019
Lake Simcoe (Canada)	Mesotrophic	Crossman & Elliott, 2018; Crossman et al., 2019
Ullswater (UK)	Oligotrophic	Bernhardt et al., 2008
Wastwater (UK)	Oligotrophic	Elliott & Thackeray, 2004
Windermere (UK)	Mesotrophic	Elliott, 2012

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345 Fig. 1 The modelled relationship between changing Loweswater catchment soluble reactive
346 phosphorus (SRP) load and annual mean concentrations of total (solid line) and cyanobacteria
347 (dashed line) chlorophyll *a*. Adapted from Norton et al. (2012) removing the individual
348 scenario data points to show only the relationships.

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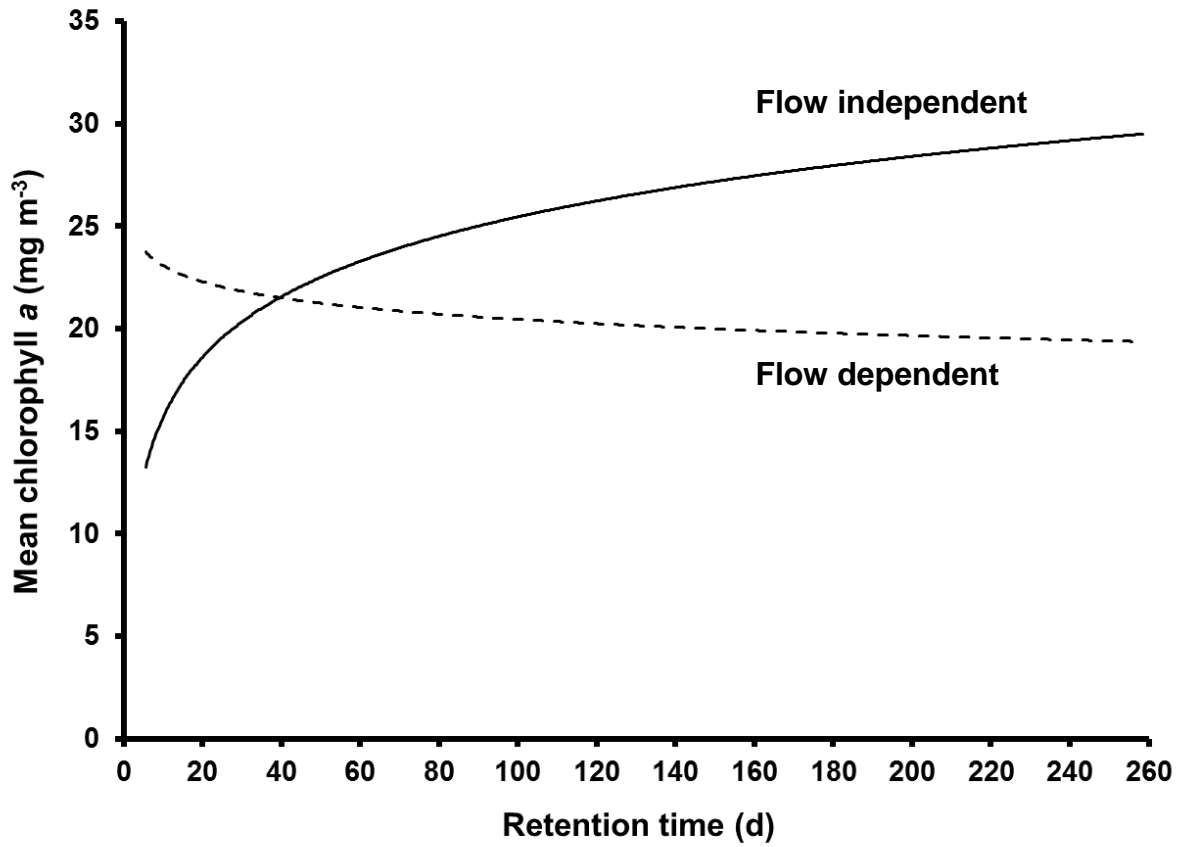
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357 Fig. 2. Illustration of the modelled relationship between summer mean chlorophyll and
358 retention time when the nutrient source for the lake is either flow independent (solid line) or
359 flow dependent (dotted line).

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