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Elliott, J. Alex. 2021. **Modelling lake phytoplankton communities: recent applications of the PROTECH model**.

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 (**P**hytoplankton **R**esp**O**nses **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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Introduction

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

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

Following this work, Reynolds went on to begin the construction of a computer model with a colleague, Anthony Irish. At its heart lies the equations of Reynolds (1989) but further enumeration was required to allow for the effects of nutrient limitation upon growth rates and various loss processes such as zooplankton grazing, sedimentation and flushing removal. With the final addition of species-specific daily vertical movements, the biological core of the new PROTECH (**P**hytoplankton **R**esp**O**nses **T**o **E**nvironmental **CH**ange) model was complete. The conception, equations and first 10 years of research of the PROTECH model was extensively reviewed in Elliott et al. (2010), but this review will consider the new PROTECH research from the last 10 years after a brief overview of the model.

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.

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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 km^2; Elliott *et al*., 2007). However, since then it has been applied to

93   the UK's largest lake, Lough Neagh (383 km^2; Elliott et al., 2016), Pyhäjärvi in Finland (154

94   km^2; Pätynen et al., 2014) and Lake Simcoe, Canada (2899 km^2; 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.

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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.

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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 <u>all</u>

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

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.

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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.

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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 km^2 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 km^2 (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 hypolinimon 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 *Plantothrix*-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 cyanobactera. Conversely, lakes that currently experience blooms

302 of low-light tolerant phytoplankton, like *Plantothrix*, might see a decline in their dominance

303 if the deeper mixing (e.g. > 10 m) seen in those lakes shallowed in the future.

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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.

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

323   phytoplankton.

Name:	*Chlorella*	*Asterionella*	*Dolichospermum*
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 (μmol photon m^{-2} 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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Table 2. List of lakes and reservoirs where PROTECH has been applied and tested in peer-reviewed studies. Studies post-2010, considered in this review, are highlighted in **bold**.
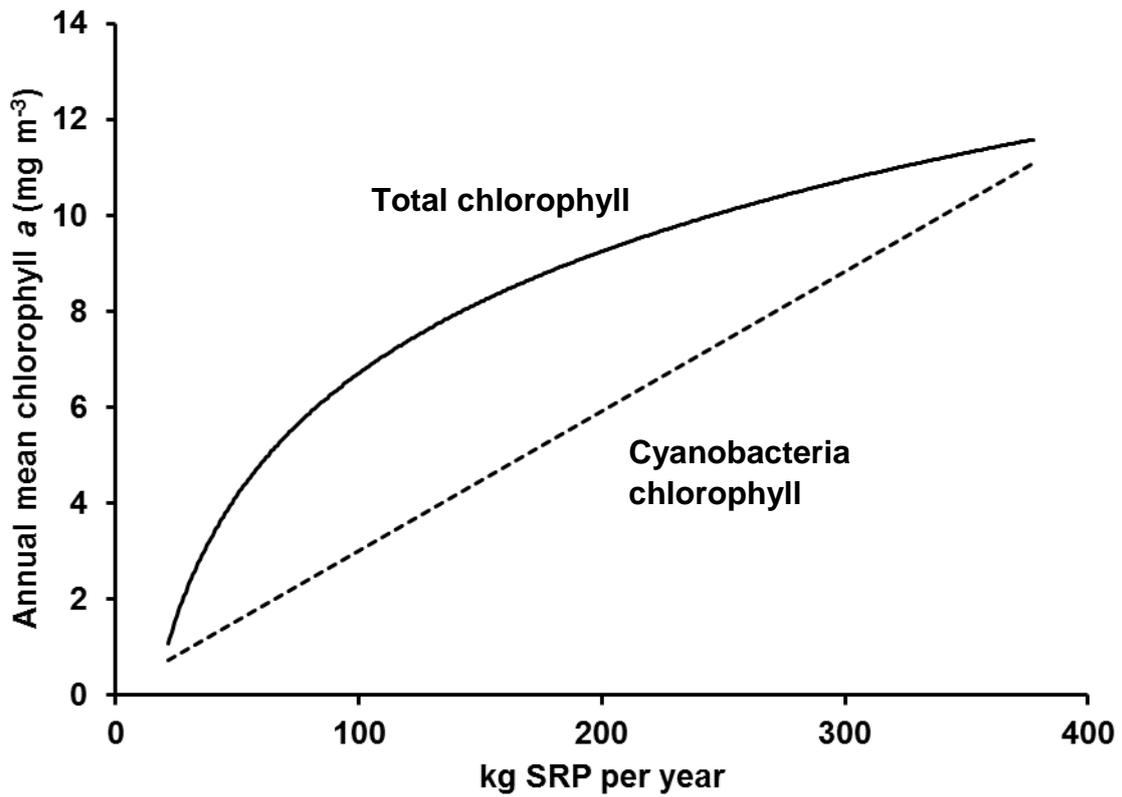
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Water body (Country)	Trophic status	Reference
Bassenthwaite Lake (UK)	Mesotrophic/Eutrophic	Elliott et al., 2006; Bernhardt et al., 2008
Blelham Tarn (UK)	Eutrophic	Elliott et al., 2000; **Gray et al., 2019**
El Gergal Reservoir (Spain)	Eutrophic	Elliott 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 at 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.
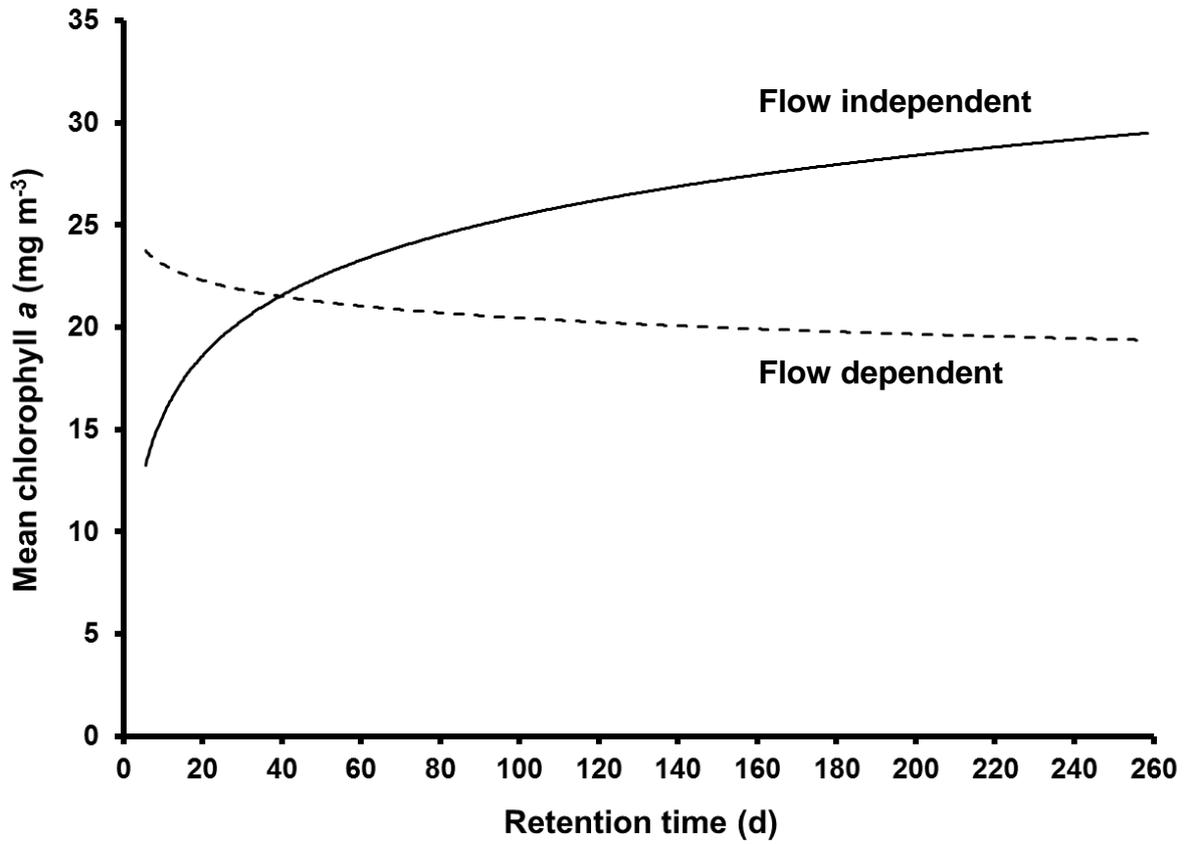
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357   Fig. 2. Illustration of the modelled relationship between summer mean chlorophyll and

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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