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1 **New, old and evergreen frontiers in freshwater phytoplankton ecology: the legacy of Colin S. Reynolds**

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16
17 **Abstract**

18
19 This paper offers a brief overview of the contributions provided by widely recognized phytoplankton
20 ecologists to honour the memory of an undisputed leader in the field of aquatic sciences: Colin S. Reynolds.
21 Colin passed away quite unexpectedly in December 2018 causing a wave of sorrow that rapidly circulated
22 among friends and colleagues all over the world. The 14 review papers collected in this Special Issue form a
23 tribute to Colin's scientific thinking, which survives the man and represents a legacy to all the scientists in
24 the field, especially to young generations. Although authors and editors carefully selected 14 different
25 topics, a certain degree of overlap exists among the collected contributions. This, far from being a limit,
26 further underlines the holistic nature of Colin's vision about phytoplankton and shows the need to develop
27 a comprehensive cultural framework when analysing this complex ecological group of organisms.

28
29 Keywords: phytoplankton, Colin S. Reynolds, aquatic ecology, holistic approach

30
31 **Introduction**

32 This Special Issue of Hydrobiologia envisages paying a tribute to the memory of a worldwide renowned
33 scientist in the field of aquatic sciences, Colin S. Reynolds, who dedicated his life to studying how evolution
34 moulds phytoplankton ecology, and how this process impacts aquatic ecosystems functioning. Colin passed
35 away on December 3rd, 2018 after being diagnosed with a liver cancer not much earlier. The sad news
36 rapidly circulated all around the world causing a wave of sorrow: in that day the community of
37 phytoplankton scientists not only had lost its uncontested leader and mentor, but also a very good friend
38 (Padisák, 2019). Colin's immense contribution to science was actually not only addressed by clarifying the
39 ecological issues related to phytoplankton, but by demonstrating that, through friendly cooperation,
40 scientists can achieve much more thoughtful results. He was an enthusiastic scientist and had the gift to
41 propagate his enthusiasm among colleagues, especially younger ones. In fact, he was always thrilled with
42 new ideas, willing to share his experience in an egalitarian way; this attitude, especially when coming from
43 a recognised and famous scientist, can be immensely attractive and rewarding for all researchers, especially
44 those at the beginning or their scientific career. To fight against the strong deprivation feeling arising from

45 his demise, several phytoplankton ecologists felt the need to commemorate their friend. Their reaction
46 produced this volume: a collection of 14 review papers dedicated to Colin Reynolds and rooted on his
47 holistic approach to phytoplankton ecology (see Reynolds, 1984a; 1997; 2006). As Colin wrote in the
48 editorial of the journal *Freshwater Reviews* 7(1) “the value of good review papers is well recognised but few
49 scientists working under today’s constraints have the opportunity to prioritise their preparation” (Reynolds,
50 2014); we therefore hope that the reader will appreciate the sense of unconditional affection to him and to
51 his memory that this volume wishes to represent.

52

53 **Contents of this Special Issue**

54 The reviews contained in this volume analyse some aspects of phytoplankton ecology and are aimed at
55 building a bridge between the knowledge shared in Colin Reynolds’ work and future developments of
56 phytoplankton ecology. As with the value of the huge amount of information contained in Colin’s papers
57 and books, it may take some time and repeated readings before deeply appreciating it, and most of the
58 “novelty” contained in very recent contributions to phytoplankton ecology already can be found,
59 sometimes in a nutshell, in Colin’s publications (see Appendix 1 for a complete list). In this sense, the
60 review by Chorus & Spijkerman (2021) is paradigmatic. These authors critically analysed the recent revival
61 of the view that the nitrogen to phosphorus ratio (N:P) can be regarded as an independent factor that
62 regulates phytoplankton assemblage composition. In fact, in a paper published more than twenty years ago
63 (Reynolds, 1999), Colin elegantly had already shown that this opinion was based on a wrong interpretation
64 of classical Tilman’s experiments (Tilman, 1977) on coexistence and competition. Moreover, he
65 demonstrated that papers that found statistical causality between the N-P ratio and the composition of
66 phytoplankton were lacking in-depth interpretation of possible alternative mechanisms. Actually, the vision
67 of Colin Reynolds, rooted in the thinking of Ramon Margalef but extremely original at the same time,
68 encompassed population and community ecology: according to Reynolds (1997, but see also Kruk et al.,
69 2021 for further insights), community assembly relies on the fact that most phytoplankton species can grow
70 under a wide range of environmental conditions. The structure of the assemblage will therefore depend
71 upon the trade-off among several complex chemical, physical and biological factors as well as upon
72 evolutionary and metacommunity processes (see the review by Rojo, 2021).

73 Most of Colin’s thinking is rooted in the definition of phytoplankton that he gave us (and that can be
74 found in the first paragraph of his 2006 book): phytoplankton is the collective of photosynthetic organisms
75 adapted to live partly or continuously in apparent suspension in the open water of the sea, of lakes, ponds
76 and rivers, and whose “swimming” ability cannot exceed turbulent entrainment. As shown in the review by
77 Naselli-Flores et al. (2021), this definition discloses several features of phytoplankton, from its “small” size
78 to its amazing, evolutionary-driven morphological variability (including colony formation, a first step to
79 multicellularity; e.g. see Xiao et al. (2018) and literature therein). The latter, in particular, results from a

80 wide range of adaptations specifically selected to live in apparent suspension in water and encompasses
81 many issues related to phytoplankton growth. Morphological adaptations often mirror physiological
82 adaptations in terms of light harvesting and nutrient uptake; these in turn allow phytoplankton to cope
83 with the aforementioned wide range of environmental conditions that characterises “average” aquatic
84 ecosystems. In particular, temperature is both an important environmental variable and a factor driving the
85 shape and size structure of phytoplankton. As discussed in detail in the first chapters of Reynolds (2006),
86 both water density and viscosity depend on temperature and hence influence the apparent suspension of
87 phytoplankton and its degree of entrainment in water motion. In fact, there is a need to reach a
88 compromise among light harvesting, uptake of nutrients and grazing resistance when transported in the
89 water motion (see the review paper by Lüring, 2021). This need, along with the wide range of resource
90 availability that can occur on the planet, has been acting as a powerful selective force on the size and
91 morphology of this group of organisms for billions of years.

92 Early in his career, Colin Reynolds was able to recognise that most of the fluctuations in resource
93 availability occurring in the majority of aquatic ecosystems could be summarised by a relatively small
94 number of life strategies. Although this way of thinking was not new in Science, he added a novel
95 perspective to the topic: when discussing about Life, exceptions are often the rule and only a holistic
96 perspective can help to identify how environmental constraints regulate phytoplankton structure and
97 dynamics. An interesting example, as George (2021) showed in his review paper, can be found by analysing
98 the complex issue related to the control exerted by “bottom-up” and “top-down” factors on phytoplankton
99 dynamics, which fed the scientific debate in the early 1990’s. The problem, as recalled by George (2021)
100 was faced by Reynolds (1994), who, in the attempt to put order in what had become quite hot topic,
101 highlighted the importance of wind-mixing intensity in modifying “expected” patterns in phytoplankton
102 dynamics. Once again Colin showed his ability in transcending what was the current scientific thinking; very
103 recently, and thanks to the increased technological skills, the scientific literature started considering the
104 multiple effects of wind-induced microscale turbulence as complex factors governing the biological
105 interactions in the plankton (see Naselli-Flores et al., 2021).

106 As reviewed by Zohary et al. (2021), temperature governs the size structure of phytoplankton in multiple
107 ways. In particular, it directly affects this group of organisms by impacting its physiology and basic
108 metabolic processes such as respiration, growth, nutrient uptake and photosynthesis. Photosynthesis is a
109 fundamental process sustaining and allowing Life on our Planet. Phytoplankton is the major contributor to
110 global photosynthesis and this primacy is achieved in an environment characterised by unpredictable light
111 fluctuations. Very often, phytoplankton ecologists seem to forget the importance of light availability (and
112 movements of water masses) for phytoplankton existence, focussing on nutrient dynamics and relying on
113 meaningless nutrient ratios to explain the structure of phytoplankton assemblages (Zohary et al., 2010). A
114 review on the aspects linked to photosynthesis, carbon acquisition and productivity in phytoplankton was

115 offered by Dokulil & Qian (2021) who also showed how primary productivity and growth are intimately
116 connected to each other, representing two sides of the same coin, and how they may depend on the
117 physical variability of the environment.

118 Physiological adaptations also play a role in allowing phytoplankton to successfully inhabit “extreme”
119 environments. As shown in the review by Padišák & Naselli-Flores (2021), harsh environments (in terms of
120 pH, light, salinity, DOC, temperature and mixing regime) host phytoplankton assemblages whose
121 composition tends towards extreme simplification (up to becoming monospecific) as the involved variables
122 are approaching the extreme of their range. However, the paper by Izaguirre et al. (2021), who reviewed
123 the extant knowledge on phytoplankton dynamics and structure in Antarctic lakes, shows that the diversity
124 of those peculiar assemblages is largely underestimated by traditional morphology-based taxonomy.

125 Understanding phytoplankton diversity and species coexistence was an important topic in Colin’s
126 research (e.g. Reynolds et al., 1993). His books (especially Reynolds, 2006) collect a huge amount of
127 information in this respect and show how much his thinking on this topic was profoundly evolutionarily-
128 focussed. In their review, Borics et al. (2021) analyse the context of phytoplankton ecology linked to the
129 mechanisms that govern its specific and functional diversity. Their approach encompasses a broad range of
130 topics, from ecological theory on species competition and coexistence to the change of diversity occurring
131 along environmental gradients, and the modelling tools used to assess diversity.

132 As reviewed by Elliott (2021), the important contribution of modelling in deciphering complex natural
133 patterns was crystal clear to Colin Reynolds who, through a series of laboratory experiments (Reynolds,
134 1989), found relationships between the growth rates of a range of different lake phytoplankton species and
135 their morphologies (Reynolds and Irish, 1997). This work represented the first step to the development of
136 the PROTECH (Phytoplankton RespOnses To Environmental CHange) model, which represents a powerful
137 and useful tool to understand lakes and their phytoplankton. As reported by Elliott (2021), who
138 collaborated with Colin in the development of the model, they used to joke that PROTECH was a digitization
139 of Colin’s brain, taking his knowledge of phytoplankton and turning it in binary digits.

140 The relationships between growth rates and morphological traits (defined as “powerful predictors of
141 optimum dynamic performance” in Reynolds et al., 2002) are also at the base of Colin’s proposal for a
142 functional classification of freshwater phytoplankton. This classification defines a number of functional
143 groups (coda) each collecting species with common morphological, physiological, behavioural and/or life
144 history characteristics (traits). The functional classification of freshwater phytoplankton, as discussed in
145 details in the review by Kruk et al. (2021), is probably the most enduring legacy of Colin Reynolds to
146 freshwater phytoplankton ecologists. The development of the theoretical framework of this classification
147 lasted more than twenty years (Reynolds, 1980; 1984b; 1997; Reynolds et al., 2002) and for another period
148 of almost twenty year it has been widely used by phytoplankton ecologists working on different kinds of
149 inland water ecosystem (both deep and shallow lakes, ponds, rivers) all around the world [when preparing

150 this text more than 1800 citations to Reynolds et al. (2002) were available in Google Scholar]. As
151 highlighted by Kruk et al. (2021), the striking success of this approach lies in the possibility to “increase the
152 predictability of phytoplankton community responses, by condensing information on many species without
153 losing their key responses - main driving mechanisms - and effects”.

154 As Abonyi et al. (2021) show in their review, the functional classification and functional group concepts
155 represented a turning point also for research addressed at studying river phytoplankton due to its close
156 resemblance to shallow lakes phytoplankton (Reynolds et al., 1994). These authors highlight how Colin
157 Reynolds thinking, building on Margalef’s thoughts about the role exerted by turbulence and incomplete
158 mixing in successive river compartments (Margalef, 1960), also contributed to solve the apparent paradox
159 of maintenance of potamoplankton populations (Reynolds, 1988). Moreover, Abonyi et al. (2021) discuss
160 how, by applying the concepts in the functional groups approach, it is possible to disentangle the effects
161 exerted by natural constraints on river phytoplankton from those caused by human impacts.

162 The impact of anthropogenic stressors (mainly eutrophication and climate change, but also the
163 spreading of non-indigenous species, and pollution from a wide array of persistent chemicals) on
164 phytoplankton composition and structure was extensively reviewed by Salmaso & Tolotti (2021). These
165 authors, by recognising the importance of the functional group approach, considered the mechanisms
166 through which human activities impact phytoplankton, how they propagate from individual to ecosystem
167 levels and what kind of alteration they induce at each level as their intensity increases. Moreover, they
168 highlight the importance of “omics” technologies (e.g. next generation sequencing and ecological
169 metabolomics) to improve the knowledge on the effects exerted on phytoplankton at different levels by
170 human-induced alterations in the ecosystem functioning.

171

172 **Conclusions**

173 The review papers contained in this Special Issue represent a tribute to the immense contributions that
174 Colin Reynolds gave to the development of both modern aquatic sciences and phytoplankton ecology,
175 although they cannot exhaustively track the depth of the ecological thinking of this great scientist. Reading
176 the literature produced by Colin Reynolds since the beginning of his scientific career, is the perfect exercise
177 for any (young) scientist who is seeking an explanation to what editors of scientific journals want when
178 asking their authors for “novelty”. The legacy that Colin has left us is actually not just a piece of knowledge
179 but his ability to find “new” perspectives when analysing “old” problems. This requires the dedication and
180 passion that arise from curiosity, and also a deep knowledge of what science has been produced in the
181 past. In this internet-dominated time it can be easy to “forget” what was done in the past simply because
182 “old” literature is often not available by browsing the web. More than often, one can happen to read
183 papers claiming new findings and then realise that what is contained there had been already published 30
184 or 40 years before by somebody else. This is partly due to the modern “hurry” culture within which many

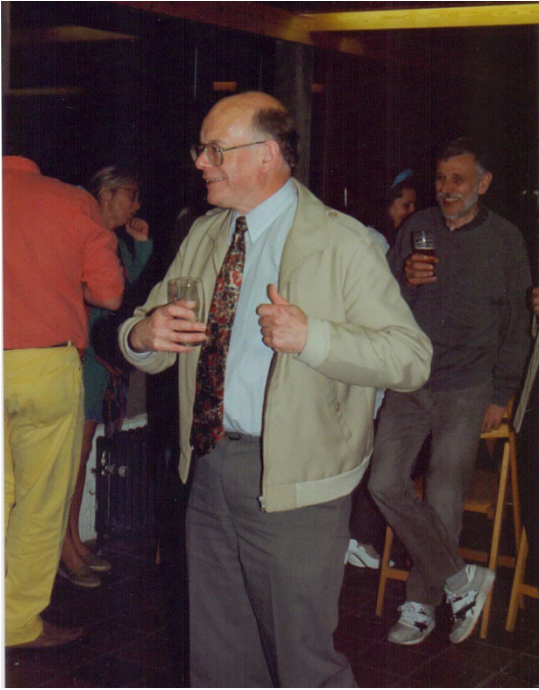
185 scientists have to publish their papers because of “evaluation procedures” and partly is a side effect of the
186 “information bombing” (very often superficial and of substandard quality) scientists are experiencing day
187 by day. We therefore would like to recommend scientists, especially younger ones, to allow themselves to
188 find the time to read the entire *corpus* of Reynolds’ literature. Actually, as claimed by Rojo & Alvarez-
189 Cobelas (2000), we still need more ecology in phytoplankton ecology, i.e. we still need Colin’s thinking to
190 find novel perspectives solidly anchored in a correct theoretical framework.

191

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260 Colin Reynolds at the 9th workshop of IAP (International Association for Phytoplankton Taxonomy and
261 Ecology) organised by J.-P. Descy and held at Mont Rigi (Belgium) in 1993. Colin was an important reference
262 for the IAP meetings and convened the 11th workshop, held in Preston Montford Field Studies Centre,
263 Shrewsbury (UK), in 1998. In this picture, taken by J.-P. Descy, it is possible to recognise Pierre Compère, co-
264 convener of the 9th IAP, and Rossella Barone.