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Phytoplankton and periphyton primary production in clear and turbid shallow lakes: influence of the light environment on the interactions between these communities --Manuscript Draft--

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Abstract:	<p>The ecological relevance of shallow lakes has been largely documented. The Pampean plain (Argentina) holds one of the main wetlands of South America, constituted by thousands of shallow lakes which provide valuable ecosystem services, and can be found in any of three regimes: clear-vegetated, inorganic-turbid or phytoplankton-turbid. Since these lakes play an important role in the global carbon balance, metabolism studies encompassing phytoplankton and periphyton under different regimes become relevant. Here, we analyzed the primary production (PP) of phytoplankton and periphyton in three Pampean shallow lakes representing the main types mentioned. The relative contribution of each algal community to the joint PP was different in each lake and related to their regime. The periphyton contribution was higher in the clear-vegetated lake than in the turbid lakes. The phytoplankton-turbid lake exhibited the highest PP for both communities. The inorganic-turbid lake presented the highest light limitation; nonetheless, the efficiency of periphyton in this lake showed an increasing trend with depth, suggesting light acclimation. Although phytoplankton dominated the PP in the three lakes, periphyton contribution was also important, particularly in the clear-vegetated lake. Our results emphasize that the PP of attached communities should be considered to estimate the PP of the whole lake.</p>	
Response to Reviewers:	<p>According to the suggestion of the Associate Editor, this version of the ms was corrected by a native English speaker.</p> <p>With my best regards, M. Laura Sánchez</p>	

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The paper has been greatly improved through the two revisions. But it cannot be published without a final edit by an English-speaking writer. There are many grammatical errors that remain in the paper. Will you be able to identify a grammar editor to work through the paper to provide that final level of changes to make the paper publishable?

Dear Editor in Chief

Dr. Marinus L. Otte

I send you the last version of our paper "Phytoplankton and periphyton primary production in clear and turbid shallow lakes: influence of the light environment on the interactions between these communities", authors: Sánchez, M. L., Rodríguez, P., Torremorell, A. M., Izaguirre, I & H. Pizarro.

This version was revised and corrected by a native English speaker in order to improve its fluency and grammar.

Best regards,

María Laura Sánchez

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1 **Phytoplankton and periphyton primary production in clear and turbid shallow**
2 **lakes: influence of the light environment on the interactions between these**
3 **communities**

4

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18

19 **Abstract**

20 The ecological relevance of shallow lakes has been largely documented. The Pampean
21 plain (Argentina) holds one of the main wetlands of South America, constituted by
22 thousands of shallow lakes which provide valuable ecosystem services, and can be
23 found in any of three regimes: clear-vegetated, inorganic-turbid or phytoplankton-
24 turbid. Since these lakes play an important role in the global carbon balance,
25 metabolism studies encompassing phytoplankton and periphyton under different
26 regimes become relevant. Here, we analyzed the primary production (PP) of
27 phytoplankton and periphyton in three Pampean shallow lakes representing the main
28 types mentioned. The relative contribution of each algal community to the joint PP was
29 different in each lake and related to their regime. The periphyton contribution was
30 higher in the clear-vegetated lake than in the turbid lakes. The phytoplankton-turbid
31 lake exhibited the highest PP for both communities. The inorganic-turbid lake presented
32 the highest light limitation; nonetheless, the efficiency of periphyton in this lake showed
33 an increasing trend with depth, suggesting light acclimation. Although phytoplankton
34 dominated the PP in the three lakes, periphyton contribution was also important,
35 particularly in the clear-vegetated lake. Our results emphasize that the PP of attached
36 communities should be considered to estimate the PP of the whole lake.

37

38 **Key words:** primary production, periphyton, phytoplankton, turbid shallow lakes, clear
39 shallow lakes

40

41 **Introduction**

42 Macrophytes and algae from plankton and periphyton are the main primary producers in
43 shallow lakes (Goldsborough and Robinson 1996). In clear shallow lakes, attached
44 algae play a major contribution to the lake's primary production (PP) (Ask et al. 2009);
45 however, their contribution to the whole ecosystem has been less investigated due to the
46 methodological constraints involved in periphyton analysis (Hansson 1992; Kalff 2003).
47 Although there has been an increase in the understanding of the role of littoral
48 periphyton in lakes (e.g. Lowe 1996; Havens et al. 2001; Vadeboncoeur and Steinman
49 2002; Vadeboncoeur et al. 2014), there is still a need for further studies on the
50 ecological regulation of PP and biomass of this community (Vadeboncoeur et al. 2014).
51 Periphyton could be a substantial component in whole-lake PP, forming part of the food
52 web base that supports a variety of fishes; thus, the inclusion of this community in
53 measurements of the energy flow of lake ecosystems is essential (Vadeboncoeur et al.
54 2008). Moreover, since shallow lakes are important contributors to the greenhouse gas
55 fluxes to the atmosphere (Cole et al. 2007; Schrier-Uijl et al. 2011), periphyton should
56 be taken into account due to its relevance in the global carbon balance.

57 The importance of light and nutrients as the main regulating factors of PP, both
58 for phytoplankton and phytoperiphyton, has been largely documented (e.g. Kirk 2011).
59 The phytoplankton absorbs and scatters light before it reaches the periphyton, which
60 limits the quantity and affects the quality of available light for attached communities
61 (Jäger and Diehl 2014). Thus, when the nutrient concentration in the water column is
62 high, phytoplankton usually dominates the lake's PP (Vadeboncoeur et al. 2003). In the
63 case of the periphyton, the relation between PP and nutrient concentration in the water
64 column seems to be substratum-dependent; particularly, soft substrata provide an extra
65 nutrient source to the attached algae that grow over them, which is an advantage for this
66 community in lakes with nutrient limitation (Hansson 1988; Burkholder 1996; Wetzel

67 2005; Vadeboncoeur et al. 2006). Competitive interactions between phytoplankton and
68 periphyton can be reflected in an inverse relationship between PP of both communities
69 through an increasing trophic gradient, i.e., shifting from systems where PP is
70 dominated by attached communities to systems dominated by phytoplankton (Hansson
71 1992; Vadeboncoeur et al. 2003; Jäger and Diehl 2014).

72 The prevalence of the different primary producers in shallow lakes has been well
73 described by the conceptual models referring to alternative equilibrium regimes
74 (Scheffer et al. 1993; Liboriusen and Jeppesen 2003; Scheffer 2009). At an intermediate
75 range of nutrient levels, two alternative regimes can occur: clear-vegetated and turbid
76 with high phytoplankton biomass (Scheffer et al. 1993; Scheffer 2009). The shift
77 between these regimes can be associated with variations in nutrient loading, changes in
78 the water level, seasonality, presence of submerged macrophytes, and fish removal,
79 among other factors (Scheffer 1998). These contrasting regimes are functionally
80 different, due to the contribution of macrophytes, periphyton and phytoplankton to the
81 whole-lake production (Genkai-kato et al. 2016). The PP of clear oligotrophic shallow
82 lakes can be dominated by attached algae, whereas that of turbid regimes is usually
83 dominated by phytoplankton. However, under eutrophic conditions, depending on light
84 availability, phytoplankton or periphyton can substantially contribute to the joint PP
85 (JPP) (i.e., periphyton plus phytoplankton PP).

86 Our study was conducted in three shallow lakes of the Pampean plain in
87 Argentina. Nowadays, most water bodies of this region are eutrophic due to human
88 activities (Quirós et al. 2006), and their waters exhibit a variety of optical characteristics
89 (Pérez et al. 2010). Most lakes are turbid due to high phytoplankton biomass
90 (phytoplankton-turbid), although a few lakes are still in a clear state and colonized by
91 submersed vegetation (clear-vegetated). The latter are located in areas with low human

92 impact, whereas phytoplankton-turbid lakes are found in highly impacted areas. These
93 types of shallow lakes fit well in the model proposed by Scheffer et al. (1993). A third
94 type of lake, less frequent in this region, is the inorganic turbid, where the high turbidity
95 is due to inorganic suspended material. Quirós et al. (2002) associated this type of lakes
96 with anthropogenic activities over their basins, which affect their water surfaces. In the
97 three types of shallow lakes, PP has been previously assessed only for phytoplankton
98 (Allende et al. 2009). Phytoplankton-turbid lakes exhibit higher values of phytoplankton
99 PP (PPP) and photosynthetic efficiency than the other two lake types. Torremorell et al.
100 (2009) measured PPP in a phytoplankton-turbid lake over an annual cycle and
101 concluded that light limits the PPP throughout the year. For the Pampean region, the
102 previous information about periphyton PP (APP) is scarce and restricted to a wetland
103 located in the Paraná River floodplain, which is strongly influenced by changes in water
104 level (Rodríguez et al. 2012; Rodríguez and Pizarro 2015). Nevertheless, for the three
105 types of Pampean shallow lakes previously described, studies on periphyton have
106 focused mainly on the structure of the community, describing changes in biomass and
107 taxonomic composition (Cano et al. 2013; Esquiús and Escalante 2012). Regarding the
108 interactions between phytoplankton and periphyton, previous studies conducted in
109 Pampean shallow lakes have shown the relative importance of these communities in
110 terms of structure under different regimes (Casco et al. 2009; Sánchez et al. 2010). The
111 JPP for both communities has been assessed only in the wetland previously mentioned
112 (Rodríguez et al. op. cit.; Rodríguez and Pizarro op. cit.), but none of these studies has
113 analyzed the contribution of each community to the algal JPP in lakes with different
114 regimes.

115 In the last years, the importance of freshwater ecosystems in the global carbon
116 balance has been highlighted (Cole et al. 2007; Tranvik et al. 2009). Particularly,

117 shallow lakes are crucial because they are widely distributed, very abundant, and
118 vulnerable to eutrophication. Lakes with contrasting regimes differ in the relative
119 contribution of the different primary producers, probably influencing their role in the
120 global balance of carbon. In this context, data on the contribution of the different
121 autotrophic compartments to the whole-lake PP become relevant.

122 The aim of this study was to compare the relationship between PPP and APP in three
123 shallow lakes from the Pampean plain with different regimes, exemplified by the
124 following lake-types i) clear-vegetated, ii) phytoplankton-turbid, and iii) inorganic-
125 turbid. Taking into account that these three types of lakes differ in the biomass of
126 phytoplankton and periphyton, we postulated that these differences will be reflected in
127 the relative contribution of each algal community to the JPP. We expected a higher
128 contribution of APP to JPP in the clear-vegetated lake than in the turbid ones.

129 **Methods**

130 *Study site*

131 The following three shallow lakes of the Pampean plain (Buenos Aires Province,
132 Argentina) were selected for the study: Kakel Huincul, El Burro and Yalca (mean depth
133 < 2 m). The choice was based on their different regimes to represent the three possible
134 scenarios for the region. Kakel Huincul (36° 48' S; 57° 47' W) is a clear-vegetated
135 shallow lake with abundant submerged macrophytes (mainly *Myriophyllum* sp. and
136 *Ceratophyllum demersum*). El Burro (35° 42' S; 57° 55' W) is a phytoplankton-turbid
137 shallow lake, which exhibits patches of emergent macrophytes in littoral zones
138 (*Schoenoplectus californicus*). Yalca (35° 35' S; 57° 55' W) is an inorganic-turbid
139 shallow lake with scarce phytoplankton and macrophytes. The location of the three
140 lakes can be seen in Fig. 1 in Sánchez et al. (2013).

141 *Environmental variables*

142 Depth-integrated water samples were taken at the beginning and at the end of the
143 colonization period to determine dissolved and total nutrients. Samples were collected
144 with a 1.5-L Plexiglass bottle in triplicate in each sampling point and transported in dark
145 and cold conditions to the laboratory. For dissolved nutrient analyses, samples were
146 filtered through Whatman GF/F filters. Nitrate + nitrite (cadmium reduction method),
147 soluble reactive phosphorus (SRP; ascorbic acid method) and ammonia (salicylate
148 method) were analyzed with a HACH DR/2010 spectrophotometer, using HACH
149 reagents. Dissolved inorganic nitrogen (DIN) was calculated as the sum of nitrate,
150 nitrite and ammonia concentrations. Total nitrogen (TN) and total phosphorus (TP)
151 concentrations were determined with the same methodology used for dissolved nutrient
152 analysis, after the digestion with boric acid and potassium persulphate. Alkalinity was
153 determined by titration with HCl 0.1 N within 24 hours (Mackereth et al. 1978).
154 Dissolved inorganic carbon (DIC) was estimated from alkalinity, pH and temperature
155 measurements (Stumm and Morgan 1996).

156 At the same sample point, conductivity, pH and temperature were measured sub-
157 superficially with a portable sensor HANNA HI991301 and dissolved oxygen (DO)
158 with a portable sensor HANNA HI9146 (HANNA Instruments, USA). Downward
159 irradiance was measured *in situ* with a spectro-radiometer USB2000 (Ocean Optics)
160 around noon. Vertical diffuse attenuation coefficient for photosynthetically active
161 radiation (K_{dPAR}) was determined as the slope of the linear regression of the natural
162 logarithm of downward irradiance profile vs depth (Kirk 2011). Turbidity was measured
163 using a HACH 2100P[®] turbidimeter. Total suspended solids (TSS) were determined by
164 filtering a known volume of water through pre-combusted and weighed Whatman GF/F

165 filters (0.7 μm nominal pore size). TSS concentration was obtained as the difference of
166 the dry filter before and after filtration (APHA 2005).

167

168 *Experimental design*

169 The PP of phytoplankton and periphyton at different depths was measured *in situ* in the
170 three shallow lakes selected, by using samples of each natural community collected
171 from each lake and applying the C^{14} methodology assimilation (see *Primary Production*
172 (*PP*) section below). The study was conducted in the mid-summer season, between
173 January 7th and January 9th, 2010.

174 For periphyton analyses, we decided to use artificial substrata to ensure a better
175 quantification of the area colonized by this community. Artificial substrata
176 (polycarbonate strips of 2.5 cm in width and 50 cm in length) were submersed vertically
177 one month before the start of the experiments to allow the community to develop. At
178 least five artificial substrata were placed in the littoral zone of each lake; each of them
179 was attached to a single wooden frame. At the beginning of the experiment, each
180 substratum was carefully cut in three sections of 8 cm: from 8 to 16 cm (depth: 8 cm),
181 from 16 to 24 (depth: 16 cm) and from 24 to 32 cm (depth: 24 cm); the upper and lower
182 portions of each substratum were discarded to ensure that the portion of the strip used
183 was always submersed and to minimize the influence of the re-suspension of bottom
184 sediment.

185

186 *Phytoplankton sampling*

187 At each shallow lake, three samples for quantitative analyses of phytoplankton were
188 sub-superficially collected with a bottle and fixed with acidified lugol (1% final
189 concentration). Counts were performed under a Zeiss inverted microscope, following
190 the methodology proposed by Utermöhl (1958); the counting error was 10%.

191 To estimate chlorophyll *a* concentration (Chl *a*), a second set of samples were collected.
192 From these samples, a known volume of water was filtered through Whatman GF/F
193 filters. Chl *a* was measured spectrophotometrically using hot ethanol (60-70 °C)
194 (Jespersen and Christoffersen 1987).

195 *Periphyton sampling*

196 Triplicate pieces of artificial substrata obtained from the original substrata cut in three
197 sections were transported in hermetic plastic bags in dark and cold conditions to the
198 laboratory, where they were scraped for estimation of Chl *a*, algal abundances and dry
199 mass fractions.

200 The attached material was suspended in a known volume of distilled water. For Chl *a*
201 analysis, we followed the same methodology used for phytoplankton by filtering the
202 material from the substrata through Whatman GF/F filters. Dry weight (DW) was
203 estimated by filtering the sample through Whatman GF/C filters (pre-combusted at 440°
204 C for 2 hours prior to use) and by weighing the material dried at 60° C in a stove. Ash-
205 free dry weight (AFDW) was determined as the mass difference after burning the
206 samples in a furnace at 440° C for 3 hours (APHA 2005). All periphyton variables were
207 referred to substrate area. In addition, the autotrophic index (AI) was estimated as the
208 AFDW:Chl *a* ratio. An AI value higher than 200 indicates a high proportion of
209 heterotrophic, non-chlorophyll organisms or organic detritus (APHA 2005). Finally,
210 substrata were scraped and the material was fixed with acidified lugol (1% final

211 concentration) for the counting of the principal taxonomic groups, in triplicate, under an
212 inverted microscope, just as for phytoplankton samples.

213

214 *Primary Production (PP)*

215 PPP and APP were simultaneously estimated in each lake, following the methodology
216 of ^{14}C assimilation as described in Holm-Hansen and Helbling (1995). The incubations
217 were simultaneously performed in duplicate at three different depths (8, 16 and 24 cm)
218 for 2 hours around noon. In the case of periphyton, we incubated the portion of the strip
219 at the same depth where it was colonized. For phytoplankton analyses, we took
220 integrated samples of the water column by means of a Plexiglass sampler device of 1.5
221 L. Owing to the polymictic and shallow characteristics of the lakes, we considered that
222 the water column was mixed. Once the incubations finished, the bottles were
223 transported to the laboratory in cold and dark conditions.

224 PPP

225 Samples were incubated in clear Plexiglass bottles (67.5 mL volume, sharp cut-off at
226 400 nm). Then, 1 μCi of $\text{NaH}^{14}\text{CO}_3$ (Perkin Elmer Life Sciences, Inc., USA) was added,
227 in darkness, to each bottle, and the bottles were incubated in the lake at different depths
228 (8, 16 and 24 cm) by means of a supporting frame. Two dark bottles containing
229 integrated water samples were also incubated. Assimilation values of transparent bottles
230 were obtained by subtracting those corresponding to dark bottles.

231 Once in the laboratory, samples were filtered through Whatman GF/F filters, and the
232 filters placed in scintillation vials in an atmosphere saturated with HCl overnight. Once
233 dried, scintillation liquid (Opti-phase Hi Safe 3, Perkin-Elmer Life Sciences, Inc.) was
234 added and the radioactivity incorporated by algae was measured using a Beckman LS-

235 6500 liquid scintillation counter. To determine the specific radioactivity in the sample, 1
236 mL of the incubated water and three drops of 0.1 N NaOH were mixed with the
237 scintillation liquid and measured as previously described.

238 The PP integrated in the water column ($\text{mg C m}^{-2} \text{ h}^{-1}$) was estimated from volumetric
239 rates ($\text{mg C m}^{-3} \text{ h}^{-1}$) at the different depth levels selected and then integrated in the water
240 column (Wetzel and Likens 2000).

241

242 APP

243 Prior to periphyton colonization, the face of each substratum that would be exposed
244 directly to solar radiation was identified with an innocuous mark. The material attached
245 to the non-exposed side was removed before the beginning of the incubation. Colonized
246 artificial substrata were introduced into incubation bottles that were identical to those
247 used for phytoplankton and placed in a similar device. Each bottle was filled with water
248 of the lake previously filtered through a 15 μm pore net to exclude most pelagic algae;
249 then, 1 μCi of $\text{NaH}^{14}\text{CO}_3$ was added to each bottle. Two dark bottles were also
250 incubated with substrata from intermediate depths. Then, the same procedure used for
251 phytoplankton samples was carried out.

252 In the laboratory, substrata were carefully scraped and the material obtained was
253 suspended in a known distilled water volume and then processed as phytoplankton
254 samples. Assimilation rates for both communities were obtained according to the
255 formula described by Holm-Hansen and Helbling (1995) and Wetzel and Likens (2000).

256 To obtain the integrated APP, PP values from the different depths were added. PPP and
257 APP were normalized to Chl *a* to be used as estimators of the production efficiency of
258 each community (hereinafter 'efficiency').

259

260 *Statistics*

261 Phytoplankton Chl *a* differences were analyzed using one-way ANOVA (factor: lakes).
262 Periphyton variables were analyzed with one-way ANOVAs (variable: Chl *a*, AFDW,
263 DW, total abundance; factor: lakes). When comparing different depths for periphyton
264 variables, two-way ANOVA was used (factors: lake and depth). PPP, APP and
265 efficiency for both communities were analyzed by means of two-way ANOVA (factors:
266 lake and depth). If necessary, data were transformed (square-root or log₁₀) to fulfil
267 assumptions of normality and homogeneity of variances. Single effects were analyzed
268 when the interaction between factors was significant. In contrast, when the interaction
269 was not significant, we used Tukey's test. SPSS and STATISTICA software packages
270 were used.

271

272 **Results**

273 *Environmental variables*

274 The higher values of DO were recorded in the phytoplankton-turbid lake; water
275 temperature was similar in the three lakes (Table 1). The conductivity values were
276 typical of lakes of this region, being lower in the inorganic-turbid lake, intermediate in
277 the phytoplankton-turbid lake, and higher in the clear-vegetated lake. The pH was above
278 8 in the three lakes (Table 1). Regarding nutrients, DIN was higher in the clear-
279 vegetated lake and lower in the phytoplankton-turbid lake, SRP ranged from 60 µg L⁻¹
280 in the phytoplankton-turbid lake to 433 µg L⁻¹ in the inorganic-turbid lake, TN was
281 higher in the clear-vegetated lake, and TP was higher in the inorganic-turbid lake (Table

282 1). The clear-vegetated lake was the clearest lake, as it can be observed from the Secchi
283 depth, turbidity, and K_{dPAR} values shown in Table 1. The phytoplankton-turbid lake
284 exhibited intermediate values of these variables, whereas the inorganic-turbid lake was
285 the most turbid lake. The highest concentration of TSS was recorded in the inorganic-
286 turbid lake (Table 1).

287

288 *Primary production (PP)*

289 Depth-integrated production for both communities showed that PPP was between 5
290 (clear-vegetated lake) and 163 (inorganic-turbid lake) times higher than APP in the
291 three shallow lakes (Fig. 1a). However, the relative contribution of periphyton to JPP
292 was higher in the clear-vegetated lake (15%), intermediate in the phytoplankton-turbid
293 lake (10%), and lower in the inorganic-turbid lake (less than 1%) (Fig. 1b).

294

295 In the clear-vegetated lake, PPP showed no differences between the three depths
296 analyzed, with averages ranging from $430 \mu\text{gC L}^{-1} \text{h}^{-1}$ to $510 \mu\text{gC L}^{-1} \text{h}^{-1}$. PPP was
297 higher in the phytoplankton-turbid lake at all depths than in the other two lakes (two-
298 way ANOVA; $F=49.1$ $p<0.004$) with the highest mean value ($1400 \mu\text{gC L}^{-1} \text{h}^{-1}$) at 16
299 cm (Fig. 2a). In the inorganic-turbid lake, we observed intermediate mean values of PPP
300 at 8 cm ($680 \mu\text{gC L}^{-1} \text{h}^{-1}$) and a significant decrease with depth (one-way ANOVA;
301 $F=169$, $p<0.001$). Thus, this was the lake with the lowest values of PPP at 16 and 24
302 cm (Fig. 2a).

303 APP was higher in the phytoplankton-turbid lake than in the other two lakes (two-way
304 ANOVA, factor lake $F=35.7$, $p<0.0001$) (Fig. 2b). In the clear-vegetated lake, APP
305 varied between $0.83 \mu\text{gC cm}^{-2} \text{h}^{-1}$ and $0.47 \mu\text{gC cm}^{-2} \text{h}^{-1}$. APP values in the
306 phytoplankton-turbid lake ranged from $1.09 \mu\text{gC cm}^{-2} \text{h}^{-1}$ to $1.24 \mu\text{gC cm}^{-2} \text{h}^{-1}$. The

307 lowest values were observed in the inorganic-turbid lake, varying between 0.015 μgC
308 $\text{cm}^{-2} \text{h}^{-1}$ near the surface and 0.006 $\mu\text{gC cm}^{-2} \text{h}^{-1}$ at deeper samples (Fig. 2b). No
309 differences were observed in APP within each lake at different depths.

310

311 The efficiency of phytoplankton (PP/Chl *a*) was higher than the efficiency of periphyton
312 in the three lakes and throughout the depth profile (Fig. 3). The highest difference
313 between phytoplankton and periphyton efficiencies was recorded in the inorganic-turbid
314 lake, where the phytoplankton:periphyton ratio efficiency varied between 12 (8 cm
315 depth) and 1021 times (24 cm depth). The efficiency of phytoplankton was similar on
316 the surface of the three lakes (Fig. 3a) but in the inorganic-turbid lake, PP/Chl *a*
317 decreased with depth (two-way ANOVA, simple effects $p < 0.005$).

318 The periphyton efficiency (PP/Chl*a*) was higher in the phytoplankton-turbid lake in
319 more superficial samples (two-way ANOVA, simple effects $p < 0.02$) (Fig. 3b). At
320 deeper samples in this lake, PP/Chl*a* decreased significantly (two-way ANOVA, simple
321 effects $p < 0.05$) but was similar to that of the other two lakes. Periphyton in the
322 inorganic-turbid lake showed increasing production efficiency with depth, although not
323 statistically significant (Fig. 3b).

324

325 *Community structure*

326 In the clear-vegetated lake, phytoplankton was dominated by filamentous Cyanobacteria
327 (80%) followed by Chlorophyceae (10%) (Fig. 4a). The phytoplankton-turbid lake was
328 represented by filamentous Cyanobacteria (50%) and Chlorophyceae (40%)
329 (unicellular, cenobial and colonial) (Fig. 4a). The inorganic-turbid lake showed the
330 lowest phytoplankton abundance, mainly represented by Bacillariophyceae (46%)
331 followed by Chlorophyceae (31%), Euglenophyceae (11%) and Cyanobacteria (10%)

332 (Fig. 4a). Phytoplankton Chl *a* showed significant differences between lakes (one-way
333 ANOVA; $F=27.09$, $p<0.05$), the mean values being higher for the phytoplankton-turbid
334 lake ($137.2 \mu\text{g L}^{-1}$) and similar between the inorganic-turbid ($73.5 \mu\text{g L}^{-1}$) and the clear-
335 vegetated ($56.4 \mu\text{g L}^{-1}$) lakes (Fig. 4b).

336 Periphyton in the clear-vegetated lake was best represented by Bacillariophyceae
337 (76.5%), followed by Cyanobacteria (18.7%), and no significant differences were
338 observed in abundance of periphyton algae with depth (Fig. 5). The autotrophic fraction
339 of the periphyton community in the phytoplankton-turbid lake was in average mainly
340 represented by filamentous Cyanobacteria (56 %), followed by Bacillariophyceae (26
341 %). Abundance showed no depth-dependent variation (Fig. 5). In the inorganic-turbid
342 lake, algal abundances decreased significantly after the first 8 cm (one-way ANOVA;
343 $F=41$, $p<0.0005$). The composition of this lake was dominated by Bacillariophyceae
344 (60.5%) and Chlorophyceae (38.8%), whose relative contribution decreased towards
345 higher depths (Fig. 5). We detected no statistical differences in total algal abundance
346 between lakes in the first 8 cm sampled; however, at deeper levels, periphyton from the
347 inorganic-turbid lake was significantly less abundant (two-way ANOVA; $F=5.6$,
348 $p<0.005$).

349 The periphyton Chl *a* of the clear-vegetated lake showed no clear pattern with depth
350 (Fig. 6). In the phytoplankton-turbid lake, periphyton Chl *a* increased significantly with
351 depth (one-way ANOVA; $F=7.2$, $p<0.05$) (Fig. 6), whereas in the inorganic-turbid lake,
352 Chl *a* decreased along with depth (one-way ANOVA; $F=27.8$, $p<0.001$) (Fig. 6). When
353 data from the three lakes were compared, the periphyton of the inorganic-turbid lake
354 contained higher Chl *a* in the first 8 cm than the other two lakes (two-way ANOVA;
355 simple effects $p<0.0001$). In contrast, the periphyton of the clear-vegetated and
356 phytoplankton-turbid lakes showed higher concentrations than the inorganic-turbid lake

357 at deeper samples (two-way ANOVA; simple effects $p < 0.0001$), without significant
358 differences between them (Fig. 6).

359 DW and AFDW in the clear-vegetated lake exhibited no statistical differences within
360 the vertical profile. The average AI in this shallow lake varied between 210 and 356;
361 these values were the lowest among the three lakes, which indicated a prevalence of the
362 autotrophic fraction in the periphyton community (Fig. 7). In the phytoplankton-turbid
363 lake, DW, AFDW and AI exhibited no significant differences with depth (Fig. 7). In the
364 inorganic-turbid lake, DW and AFDW showed a significant decrease after the first 8 cm
365 depth (one-way ANOVA; $F=18.9$, $p < 0.005$ and $F=87.9$, $p < 0.00005$, respectively). The
366 mean AI in this lake increased from 238 in the samples closer to the surface to 1841 in
367 the deepest ones, thus evidencing an increase in the heterotrophic metabolism of the
368 periphyton with depth (Fig. 7).

369

370 **Discussion**

371 Our study showed that the lake regime (clear or turbid) influences the relative
372 importance of PPP and APP in the shallow lakes of the region studied. In turbid lakes,
373 under light-limiting conditions for periphyton, phytoplankton dominated the JPP,
374 whereas in clear shallow lakes, with higher availability of light, the role of periphyton in
375 the total algal productivity acquired higher relevance.

376 The contrasting regimes of the shallow lakes studied are evidenced from the
377 environmental variables measured during this study, which are in line with previous
378 information (Allende et al. 2009; Sánchez et al. 2013). According to our data and
379 previous studies, Kakel Huincul can be classified as a typical clear vegetated shallow
380 lake, where algal communities are not limited by light or nutrients. However, during the
381 present study, several stands of submerged macrophytes were lost and the lake exhibited

382 higher turbidity, K_{dPAR} , and nutrient concentrations than in the previous surveys.
383 Probably, at the moment we performed our experiment, this lake was at the early stages
384 of a transition towards a turbid regime. On the other hand, the phytoplankton-turbid lake
385 (El Burro) exhibited intermediate nutrient values that were not limiting for algal growth
386 according to the ranges proposed by Reynolds (2006). The inorganic-turbid lake (Yalca)
387 was the most turbid lake of the ones studied and probably light- but not nutrient-
388 limited. Although both phytoplankton- and inorganic-turbid lakes exhibit high turbidity,
389 they show different optical light conditions due to the distinct origin of the suspended
390 material (Pérez et al. 2010).

391 As we expected, the attached community had a comparatively higher percentage of
392 contribution to the JPP in the clear shallow lake than in the turbid ones. Our estimations
393 are conservative considering that they were obtained using artificial substrata. If we
394 consider the periphyton growing on the natural substrata, we will expect even a higher
395 importance of the relative contribution of periphyton to the JPP, due to several factors:
396 higher availability of substrata, provision of refuge for plankton grazers and production
397 of allelopathic substances by macrophytes (Scheffer et al. 1993). Nevertheless, the use
398 of artificial substrata for periphyton studies is widely applied due to the sampling
399 simplicity and high accuracy in the measurements (Kalff 2003). The higher importance
400 of the attached communities in clear vegetated lakes could be explained by the existence
401 of competitive interactions between phytoplankton and periphyton communities
402 (Hansson 1988; Jäger and Diehl 2014). In highly productive lakes, where phytoplankton
403 has a proper access to nutrients, light may become the limiting resource for periphyton
404 development due to the shadow effect caused by phytoplankton. On the other hand, in
405 clear lakes, where periphyton is not light limited, this community can attain a better
406 development. Furthermore, it has been reported than periphyton is less sensitive than

407 phytoplankton to low nutrient concentrations in the water column (Hansson 1992).
408 Studies suggest that the relation between periphyton and nutrients in the water column
409 is influenced by the type of substrata (Vadeboncoeur et al. 2006). The dominance of any
410 productive community in shallow lakes is determined by the trophic state of the water
411 body and the benthic production decreases with the increase in the trophic level of the
412 lake due to the light attenuation caused by the large phytoplankton biomass
413 (Vadeboncoeur et al. 2008). Considering the integrated JPP, the values recorded were
414 highest in the phytoplankton-turbid lake, intermediate in the clear lake, and lowest in
415 the inorganic-turbid one. If we neglect the contribution of periphyton to the lake's JPP,
416 the whole picture would not change, but the JPP would be underestimated.

417 The clear-vegetated lake showed the lowest PPP, without differences through the depth
418 profile. In this lake, light penetrates more deeply than in the other two lakes, thus
419 phytoplankton may capture light at deeper layers, producing a relatively homogeneous
420 profile in PPP. Despite the clear regime of this lake, Cyanobacteria were very abundant
421 in the phytoplankton, probably because at the moment of our experiment the lake
422 exhibited a more turbid condition than in previous studies conducted in this water body.

423 Regarding periphyton, in this lake, the intermediate and almost constant values of APP
424 and Chl *a* along depth are explained by the better light conditions in its water column.

425 In the phytoplankton-turbid lake, Cyanobacteria and Chlorophyceae dominated the
426 phytoplankton community, in agreement with that reported in previous studies of
427 phytoplankton-turbid lakes of the region (e.g. Allende et al. 2009; Izaguirre et al. 2012).
428 This shallow lake presented the highest values of phytoplankton and periphyton
429 biomass (Chl *a*), PPP and APP. Despite the turbid characteristics of this lake, with
430 potential limiting light conditions, the PPP and phytoplankton Chl *a* increased at deeper
431 layers, which suggests a photo-acclimation process. In this sense, under critical light

432 conditions, phytoplankton might experience changes at different levels (morphological,
433 cellular or physiological) to maximize the use of the scarce available light (Falkowski
434 and LaRoche 1991). Conversely, the lower PPP on the surface of this turbid lake could
435 be due to photo-inhibition, as observed in another turbid water body of the region
436 (Torremorell et al. 2009). Besides the high periphyton biomass recorded in this lake, we
437 observed an increase in the autotrophic components of this community with depth (i.e. a
438 decrease in AI). This could imply an increase in the relative proportion of the
439 autotrophic fraction within the periphytic matrix or an increase in the quantity of Chl *a*
440 present in periphytic algae. Cyanobacteria and Bacillariophyceae, the main taxonomic
441 groups in periphyton of this lake, are considered as good competitors under critical light
442 conditions (Hill 1996; Huisman et al. 1999). Taking into account the high values of PPP
443 and APP observed in this lake, we assume that the algae living in this environment are
444 very well adapted to the turbid conditions, which seems to indicate a good combination
445 of light and nutrients for their growth.

446 In the inorganic-turbid lake, the sharp decrease in PPP with depth is explained by the
447 severe light limitation. Bacillariophyceae, which dominated phytoplankton in this lake,
448 have been frequently reported as organisms adapted to poor light conditions (Reynolds
449 2006; Kirk 2011). The lowest values of APP in this shallow lake are also related to the
450 high turbidity. Our results are in agreement with the observations of Vadeboncoeur et
451 al. (2008), who pointed out that the increase of non-organic turbidity in a lentic water
452 body reduces the total PP of pelagic and attached microalgal communities. In our study,
453 periphyton biomass decreased drastically in deeper samples, while the proportion of
454 heterotrophs increased (higher AI). Conversely, the efficiency of the periphyton in this
455 inorganic-turbid lake showed an increasing trend with depth, which seems to be
456 evidence of an acclimation process of the sessile community.

457 In general, results of the comparison of the PPP measured in the three lakes studied
458 reinforce the patterns described by Allende et al. (2009) for the same region, who
459 reported that turbid lakes are more productive than clear vegetated lakes. Regarding
460 APP, we found that the contribution of periphyton in these lakes is important, especially
461 in scenarios without light limitation; in this sense, this community should be considered
462 in future studies of shallow lakes to achieve a prospect of the whole PP in these aquatic
463 systems.

464 Our study constitutes the first comparative analysis of the PP involving both
465 phytoplankton and periphyton for shallow lakes of the Pampean plain with contrasting
466 regimes. Shallow lakes are the main freshwater environments of this productive region
467 of Argentina, and are very relevant due to their ecosystem services (recreational use,
468 fishing, irrigation, and biodiversity conservation, among others). All these water bodies
469 are subjected to the human impact, particularly agriculture and stockbreeding practices,
470 which have been intensified during the last years. As a consequence, the number of
471 turbid systems in the region has increased (Quirós et al. 2006; Kosten et al. 2012;
472 Diovisalvi et al. 2015), modifying both the PPP and the APP. In these ecosystems
473 subject to human-induced changes, long-term monitoring of the relative contribution of
474 these communities to the whole-lake PP is crucial.

475

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632

633

634 **Tables**

635 Table 1: Environmental variables measured in the lakes studied. DO: dissolved oxygen;
 636 DIN: dissolved inorganic nitrogen; SRP: soluble reactive phosphorus; TN: total
 637 nitrogen; TP: total phosphorus; TSS: total suspended solids. Values between
 638 parentheses correspond to the beginning and the end of the colonization period of
 639 periphyton, respectively. TN and TP were measured at the end of the colonization
 640 period, whereas TSS was measured at the beginning of the colonization period.

	Kakel Huincul (clear- vegetated)	El Burro (phytoplankton- turbid)	Yalca (inorganic-turbid)
Temperature (°C)	(23.5-25.8)	(25.0-28.2)	(25.0-26.2)
DO (mg L ⁻¹)	(6.7-8.2)	(11.1-12.9)	(8.9-8.2)
Conductivity (µS cm ⁻¹)	(3930-4950)	(2020-2610)	(1480-1699)
pH	(8.9-8.5)	(9.1-9.0)	(8.9-8.4)
DIN (µg L ⁻¹)	(46-155)	(70-45)	(103-80)
SRP (µg L ⁻¹)	(103-95)	(93-60)	(433-360)
TN (µg L ⁻¹)	8800	2100	2000
TP (µg L ⁻¹)	260	155	705
Secchi depth (cm)	(32-26)	(13-16)	(2-3)
K _d PAR (m ⁻¹)	(5.9-8.6)	(16.1-13.3)	(79.1-65.9)
Turbidity (NTU)	(22-28)	(128-81)	(1036-390)
TSS (mg L ⁻¹)	41.0	166.5	1052

641

643 **Figure captions**

644 **Fig.1** a) Mean primary production (PP) of phytoplankton and periphyton integrated over
645 the water column + 1 SD; b) Relative contribution of each community to the total PP.

646

647 **Fig.2** Primary production of phytoplankton and periphyton + 1 SD at depths of 8 cm, 16
648 cm and 24 cm in the three shallow lakes studied; a) Phytoplankton Primary Production
649 (PPP); b) Periphyton Primary Production (APP).

650

651 **Fig.3** Phytoplankton and periphyton efficiency (PP/Chl a) + 1 SD at depths of 8 cm, 16
652 cm and 24 cm in the shallow lakes studied; a) Phytoplankton efficiency; b) Periphyton
653 efficiency.

654

655 **Fig.4** a) Abundances of the main phytoplankton groups in the three shallow lakes
656 studied; b) Phytoplankton Chl a + 1 SD in the three shallow lakes studied.

657

658 **Fig.5** Abundances + 1 SD of the main periphyton algal groups (abundance > 1%) in the
659 three shallow lakes at depths of 8 cm, 16 cm and 24 cm.

660

661 **Fig.6** Periphyton Chl a concentration + 1 SD in the three shallow lakes studied at depths
662 of 8 cm, 16 cm and 24 cm.

663

664 **Fig.7** Periphyton average dry weight (DW), ash-free dry weight (AFDW) and
665 autotrophic index (AI) in the three shallow lakes studied at depths of 8 cm, 16 cm and
666 24 cm. Left panel: Average DW and AFDW, both + 1 SD. Right panel: AI + 1 SD

667













