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1 **Clearance rates of freshwater bivalves *Corbicula fluminea***
2 **and *Utterbackia imbecillis* in the presence and absence of light**

3

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24

25 **Abstract**

26 Light affects bivalve behavior and gaping activity, but its potential effects on bivalve filtration remain
27 poorly investigated. In this study, clearance rates of two bivalve species: the Asian clam, *Corbicula*
28 *fluminea* and paper pondshell, *Utterbackia imbecillis* were assessed in light ($6.5 \pm 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$) and
29 dark ($0.0 \mu\text{mol m}^{-2} \text{s}^{-1}$) conditions. We found that clearance rates remained similar between *C. fluminea* (50
30 $\pm 18 \text{ mL g}^{-1} \text{ h}^{-1}$) and *U. imbecillis* ($41 \pm 10 \text{ mL g}^{-1} \text{ h}^{-1}$) during light conditions. However, *C. fluminea* (110
31 $\pm 15 \text{ mL g}^{-1} \text{ h}^{-1}$) filtered significantly faster than *U. imbecillis* ($24 \pm 6 \text{ mL g}^{-1} \text{ h}^{-1}$) in the dark condition ($p <$
32 0.05). The results indicated that light might affect the filtration activity in freshwater bivalves differently,
33 depending on species.

34

35 **Keywords:** Dark, filtration rate, light, mussel, Unionidae

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45

46 **Conflict of Interest**

47 Authors declare no conflict of interest.

48

49 **Availability of data and materials**

50 Data will be available upon request.

51

52 **Authors' contributions**

53 ADH planned and conducted experiments, supervised by TJM. DH helped provide *U. imbecillis*. ADH
54 and SP analysed data, conducted statistical analysis, and wrote the paper. DH and TJM helped revise
55 writing.

56 **Introduction**

57 North America has the highest diversity of freshwater mussel species in the world, but over the past several
58 decades these animals have become among the most threatened group of organisms globally with over 70%
59 of species vulnerable to extinction or already extinct (Vaughn & Taylor 1999; Haag & Williams 2014).
60 Bivalves are filter feeders and play important roles in freshwater ecosystems through biogeochemical
61 cycling of nutrients and contaminants (Geist 2010; Haag 2012). Therefore, they are increasingly used as
62 sentinels of water quality in ecological remediation of contaminated aquatic systems (Rosa et al. 2014;
63 Otter et al. 2015). Studies on filtration rates (FRs) in freshwater bivalves under different environmental
64 conditions are needed to assess their ecological impact and potential use in bioremediation.

65 Current knowledge of the FRs of freshwater bivalve species in North America is based on a limited number
66 of species. While a considerable amount of data has been published on FRs of exotic *C.*
67 *fluminea* and *Dreissena* species (Marescaux et al. 2016; Pigneur et al. 2014; Rosa et al. 2014; Viergutz et
68 al. 2012), much less attention has been paid to native freshwater mussels, particularly Unionid species.
69 Approximately only 8 species of freshwater mussels have been studied for FR assessment in laboratory
70 experiments in North and South America (Table 1).

71 *C. fluminea* has negatively impacted native bivalve abundance and diversity in North
72 American freshwater ecosystems (Ferreira-Rodriguez et al. 2018). The FR of *C. fluminea* is often reported
73 to explain their ability to compete with other bivalve species (Pigneur et al. 2014). Several studies,
74 conducted mostly in the laboratory, have reported a wide range of individual FRs for *C. fluminea*,
75 between 29 and < 3000 mL ind⁻¹ h⁻¹ (Viergutz et al. 2012) while FRs in Unionidae usually
76 ranges between 18 and 2000 mL ind⁻¹ h⁻¹ although FRs up to <10,000 mL mL ind⁻¹ h⁻¹ were measured in
77 large individuals (up to 259 g, Table 1). Nevertheless, very few studies assessed the FRs of the different
78 species at the same time while using the same protocol, making it difficult to compare experimental data
79 (Marescaux et al. 2016).

80 Laboratory studies have highlighted that FRs in freshwater mussels vary depending on biotic and abiotic
81 factors. These include food availability, sex and reproductive cycle (Tankersley 1996; Gatenby et al.

82 2013), pH, temperature, turbidity and water velocity (Loayza-Muro and Elias-Letts 2007; Mistry and
83 Ackerman 2018; Tuttle- Raycraft and Ackerman 2019). Gatenby et al. (2013) found that *Villosa iris*
84 adjusted FRs depending on the availability of food. More recently, Mistry and Ackerman (2018)
85 experimentally assessed FRs in four Unionidae species and found that FR increased with water velocity and
86 algae flux up to a saturation level.

87 Field studies have revealed seasonal changes in FRs in several bivalve species. Viergutz et al.
88 (2012) found that seasonal variability of FR in *C. fluminea* surpasses direct temperature effects.
89 These findings demonstrate that other factors besides temperature and body mass can strongly affect FRs.
90 Additionally, light is also known to affect the behavior of bivalves involving closure or retraction of siphon
91 and valve adduction (Wilkens 2008). Morton (2008) reported that photoreceptors in bivalves are not
92 uncommon. However, no experimental study has been conducted to assess the effects of light intensity on
93 the FRs of freshwater bivalves.

94 In this study, we aimed to determine the FRs of an invasive species *C. fluminea* and a poorly studied native
95 species *U. imbecillis* under controlled light conditions. Filtration activity was assessed through the
96 determination of clearance rates of the studied species (i.e. volume of water cleared of suspended particles
97 per unit of time (Riisgård 2001).

98

99 **Methods**

100 **Bivalves and algae culture**

101 Adult *C. fluminea* and *U. imbecillis* were used to compare FRs in native and invasive species. All the
102 bivalves were collected in the field in July 2018. *C. fluminea* (weight: 3.50 ± 0.35 g wet wt, shell length:
103 20.2 ± 0.9 mm) were collected from Sewee Creek in Meigs county, TN, USA while *U. imbecillis* (weight:
104 21.2 ± 8.2 g wet wt, shell length: 62.8 ± 7.6 mm) were collected by Tennessee Wildlife Resources Agency
105 (TWRA) from Sumner Sportsman Club Lake in Portland, TN, USA and brought to the laboratory in a
106 cooler with a bubbler. No mortality was recorded during transportation.

107 The bivalves were kept in a 450-L tank (flow-through circuit of dechlorinated tap water, water renewal: 50-
108 170 L h⁻¹; ambient temperature: 14-28 °C; light intensity: 13-24 μmol m⁻² s⁻¹; light/dark: 14h/10h) and
109 acclimated to laboratory conditions for four weeks prior to the experiment. Two weeks prior to each test,
110 bivalves were fed a daily ration of a mix of the chlorophyte *Chlamydomonas reinhardtii* and the diatom
111 *Navicula sp.* (3 - 5 x 10⁶ cells g⁻¹ d⁻¹) using medical IV drip bags for continuous feeding.

112 The unicellular green algae, *C. reinhardtii* (5-6 μm of diameter) was reported to be efficiently filtered by
113 both clams and mussels (Boltovskoy et al. 1995; Gatenby et al. 1996) and was used in this clearance rate
114 experiments. *C. reinhardtii* was cultured in 10-L clear Nalgene carboys containing WC medium
115 (temperature: 23-24°C; light intensity: 150-200 μmol m⁻² s⁻¹; light/dark: 12h/12h). Algal concentrations
116 were evaluated by counting cells using a flow imaging cytometer (FlowCam® Benchtop B3 Model).

117

118 **Experimental procedures**

119 Clearance rates of each species were determined following the methods of Riisgård (2001). Individuals of
120 both species were placed in separate clear plastic containers with dechlorinated tap water (100 mL in round
121 punch cups for *C. fluminea* and 500 mL in Lee's specimen containers for *U. imbecillis*) with aeration. One
122 container was kept with no bivalve and used as a control. Preliminary tests were carried out and confirmed
123 that there was no significant difference in cell concentrations between control containers (without bivalves,
124 n = 3), so we used only one control container for each of the experiments. Bivalves were allowed to
125 acclimate until active filtering was observed (approx. 30 min).

126 After the acclimation period, live *C. reinhardtii* was centrifuged (5000 RPM for 5 min) and spiked to each
127 plastic container to reach the targeted initial concentrations. The use of concentrated algae allowed for the
128 reduction of spike volume (approximately 3 mL) and to avoid significant changes of water volume and
129 physio-chemical parameters. Subsamples of 1 mL water were taken from each plastic container five minutes
130 after the algae spike and then at 5 to 15 min intervals (based on visual color changes in the plastic
131 containers). The filtration was assessed for up to 1 h. The same sampling procedures were conducted for

132 the experiments in the dark condition where no visual observation was possible. Samples were placed in
133 1.5-mL tubes with 200 μL of 10% formalin solution and mixed immediately. Analyses of the samples were
134 performed using by flow imaging cytometry (FlowCam® Benchtop B3 Model).
135 The experiments were performed for both species in the dark ($0.0 \mu\text{mol m}^{-2} \text{ s}^{-1}$) with the initial cell
136 concentrations of *C. reinhardtii* ($2.5 \pm 0.2 \times 10^5 \text{ cells mL}^{-1}$) and in the light ($6.5 \pm 0.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$) with the
137 initial cell concentrations of *C. reinhardtii* ($4.0 \pm 0.2 \times 10^5 \text{ cells mL}^{-1}$). The sample sizes, the number of
138 individuals tested per treatment, ($n = 7$ in dark, 8 in light for *C. fluminea* and $n = 6$ in dark, 8 in light for *U.*
139 *imbecillis*) followed the recommendations from (Salerno et al. 2018). Light intensity was measured using
140 a PAR meter (Quantum Flux® Apogée). Temperature was maintained at $22 \pm 0.5 \text{ }^\circ\text{C}$ during the experiment.
141 Dark experiments were done in the evening, after the daily acclimated dark time began. Likewise, light
142 experiments were done during the day according to the acclimation period light pattern.
143 Algae concentrations in a similar range showed no influence on growth and survival of juvenile mussels of
144 *V. iris* ($3.5 \times 10^4 - 1.8 \times 10^5 \text{ cell mL}^{-1}$) (Hua et al. 2013). However, Gatenby et al. (2013) found that high
145 and low food concentration can affect FR of adult *V. iris*. So in the present study, since cell concentrations
146 of *C. reinhardtii* differed for the experiments performed in light and dark conditions, the effects of light
147 and dark condition on FRs within the same species were not evaluated statistically. Only the FRs between
148 species within the same light condition (light and dark) were statistically tested.

149

150 **Data analysis**

151 Cell concentrations (cells mL^{-1}) were analyzed in time (minutes) series. Kinetics were fitted with an
152 exponential model and linearized by log transformation. Only regressions with $R^2 \geq 0.85$ were considered
153 for clearance rate calculations (Hansen et al. 2011).

154 Clearance rates (expressed as $\text{mL g}^{-1} \text{ h}^{-1}$) were calculated according to the following equation (Mistry and
155 Ackerman 2018):

$$156 \quad CR = \frac{V}{nt} \left(\ln \frac{C_i}{C_f} - \ln \frac{C'_i}{C'_f} \right)$$

157 Where V is the volume of water in the plastic container (mL), n is the number of individual per container, t
158 is the time of the experiment (h), C_i and C_f are initial and final cell concentrations respectively in the
159 container with bivalves while, and C'_i and C'_f are initial and final cell concentrations respectively in the
160 containers used as controls (with no bivalve). The result from this equation was then divided by the total
161 wet weight (g) of the corresponding individual to normalize results from these two differently sized species.
162 Kinetics of FRs were fitted using nonlinear regression routines and iterative adjustment. Nonlinear
163 regressions and statistics were performed in R freeware 3.5.2 (R Development Core Team 2020).
164 Data for clearance rates were first tested for normality (Shapiro's test). A Student's t-test was then used to
165 assess significance of differences between the two species ($\alpha = 0.05$).

166

167 **Results and Discussion**

168 We found that *C. fluminea* filtered significantly faster ($110 \pm 15 \text{ mL g}^{-1} \text{ h}^{-1}$, $n = 7$) than *U. imbecillis* ($24 \pm$
169 $6 \text{ mL g}^{-1} \text{ h}^{-1}$, $n = 6$) in the dark condition ($t = 12.64$, $p < 0.001$). During light conditions, no significant
170 difference was found in clearance rates in *C. fluminea* and *U. imbecillis* ($t = 1.27$, $p = 0.23$) although the
171 average clearance rates were slightly higher in the *C. fluminea* ($50 \pm 18 \text{ mL g}^{-1} \text{ h}^{-1}$, $n = 8$) than those in the
172 *U. imbecillis* ($41 \pm 10 \text{ mL g}^{-1} \text{ h}^{-1}$, $n = 8$) (Fig. 1).

173 This noticeable difference of FRs in the dark was also revealed in the filtration kinetics of the two species
174 (Fig. 2). The cell concentration of *C. reinhardtii* decreased rapidly in the cups with *C. fluminea*, while it
175 did not show the same pattern in containers with *U. imbecillis* in the dark condition. During the first 20
176 minutes, *C. fluminea* filtered more than 50% of *algal* cells while *U. imbecillis* only filtered less than 25%.
177 At the end of the filtration period in the dark, only $4 \pm 2\%$ of *C. reinhardtii* cells remained in the cups with
178 *C. fluminea* while $36 \pm 8\%$ of *C. reinhardtii* cells remained in the cups with *U. imbecillis*. Filtration patterns
179 in the light remained very similar between the two species. The results indicated that *C. fluminea* had much
180 higher FRs (over 4.5 times) than *U. imbecillis* during the dark condition in this study. This finding suggests
181 that the FRs of the invasive species *C. fluminea* may be advantageous at night compared to native species.

182 FRs of *C. fluminea* in this study agree with previous measurements conducted in laboratory settings (78-
183 486 mL ind⁻¹ h⁻¹) (see Marescaux et al. 2016 for review). The FRs in *U. imbecillis* (360-1169 mL ind⁻¹ h⁻¹)
184 are close to those in other Unionidae species (Table 1), (Mistry and Ackerman 2018; Tuttle-Raycraft and
185 Ackerman 2018, 2019). There are only a few studies on freshwater bivalve filtration regarding the influence
186 of light, most of which focus on invasive species. Ortmann and Grieshaber (2003) used gaping activity in
187 *C. fluminea* to estimate filtration activity in the field and reported a circadian rhythm with valves being
188 closed in the morning and opened in the afternoon. They assumed this phenomenon was due to the food
189 availability. The invasive golden mussel *Limnoperna fortunei*, voluntarily detached its byssal threads,
190 crawled, and reattached more often in darkness than in light (Duchini et al. 2015) while invasive zebra
191 mussel *Dreissena polymorpha* and quagga mussel *D. rostriformis bugensis* showed no preference between
192 light regimes in byssal thread production (Grutters et al. 2012). Kobak and Nowacki (2007) found that *D.*
193 *polymorpha* tried to avoid any light. Altogether, these contrasting results indicate that response to light in
194 FRs in bivalves is species-dependent.

195 Limited investigations have been performed to study light effects in Unionids. Nevertheless, Haag and
196 Warren (2000) studied mantle lure displays as an endpoint for the combined effects of light and fish
197 presence in *Villosa nebulosa* and *V. vibex*. They found that presence or absence of fish had no effect on
198 display, but *V. nebulosi* displayed mainly at night while *V. vibex* displayed mainly during daytime
199 suggesting that behavior of Unionids species may be affected by light. In our study, *C. fluminea* exhibited
200 higher FRs than the Unionid *U. imbecillis* in the dark. This exotic species was already known for its high
201 FRs as well as for its ability to feed on smaller particles than most native freshwater bivalves such as
202 Unionidae (Marescaux et al. 2016 and citations within). The two species in this study can occupy the same
203 habitat and burrowing depth. While our organisms did not originate from the same location and competition
204 was not analyzed in our study, food competition would be possible in their natural habitat. Our study could
205 provide preliminary data for light conditions under which competition might occur.

206 This study provides new insights regarding the influence of light on the filtration activity of two bivalve
207 species, *C. fluminea* and *U. imbecillis*, highlighting the complexity of bivalve behavioral response to light
208 and suggests differing niche capabilities between them.

209

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307

308 **Table 1** Filtration rates of freshwater mussels from North and South America measured in various
 309 experimental studies.

Species	Shell length (mm)	Whole body wet weight (g)	Filtration rates (mL ind ⁻¹ h ⁻¹)	Reference
<i>Actinonaias ligamentina</i>	-	54-159	2700-11000*+	(Baker & Hornbach, 2001)
<i>Amblema plicata</i>	-	78-259	800-5000*+	(Baker and Hornbach 2001)
<i>Anodontites trapesialis</i>	90-100	-	700-1000	(Loayza-Muro and Elias-Letts 2007)
<i>Lampsilis fasciola</i>	67 ± 101	-	500-2000*	(Mistry and Ackerman 2018)
	51-79	-	250-650*	(Tuttle-Raycraft and Ackerman 2018)
	0.3-0.4	-	< 1**	(Mistry & Ackerman 2017)
<i>Lampsilis siliquoidea</i>	112 ± 83	-	600-2000*	(Mistry and Ackerman 2018)
	95-123	-	400-900*	(Tuttle- Raycraft and Ackerman 2018)
	80-110	-	300-1200*	(Tuttle-Raycraft and Ackerman 2019)
	0.3-0.4	-	< 3**	(Mistry and Ackerman 2017)
<i>Ligumia -suta</i>	58 ± 62	-	200-500*	(Mistry and Ackerman 2018)
	50-70	-	150-300*	(Tuttle-Raycraft and Ackerman 2018)
	0.2	-	< 1**	(Mistry and Ackerman 2017)
<i>Pyganodon cataracta</i>	-11.5-15.5	-	500-2000*	(Tankersley 1996) (Tankersley & Dimock 1993)
<i>Villosa iris</i>	37-51	-	18-55*	(Gatenby et al. 2013)
	60 ± 45	-	250-400*	(Mistry and Ackerman 2018)
	53-68	-	150-200*	(Tuttle-Raycraft and Ackerman 2018)
	0.4	-	< 2**	(Mistry and Ackerman 2017)

310 * Graphical estimation

311 ** Measured on new metamorphosed mussels

312 + Estimated from mL g⁻¹ h⁻¹ with average weight

313 **Figure captions**

314

315 **Fig. 1** Clearance rates assessed for the two tested species (the Asian clam *Corbicula fluminea* in dark gray
316 and the paper pondshell *Utterbackia imbecillis* in light gray) between August 2018 and March 2019 under
317 two light intensity conditions: (A) “Light” ($6.5 \pm 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$) and (B) “Dark” ($0.0 \mu\text{mol m}^{-2} \text{s}^{-1}$).
318 Whiskers indicate the minimum and maximum values, black lines indicate the median, and boxes represent
319 25th and 75th percentile.

320

321 **Fig. 2** Combined kinetics of all FRs for the two tested species *Corbicula fluminea* and *Utterbackia*
322 *imbecillis* under two light conditions: (A) “Light” ($6.5 \pm 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$) and (B) “Dark” ($0.0 \mu\text{mol m}^{-2} \text{s}^{-1}$).
323 ¹).

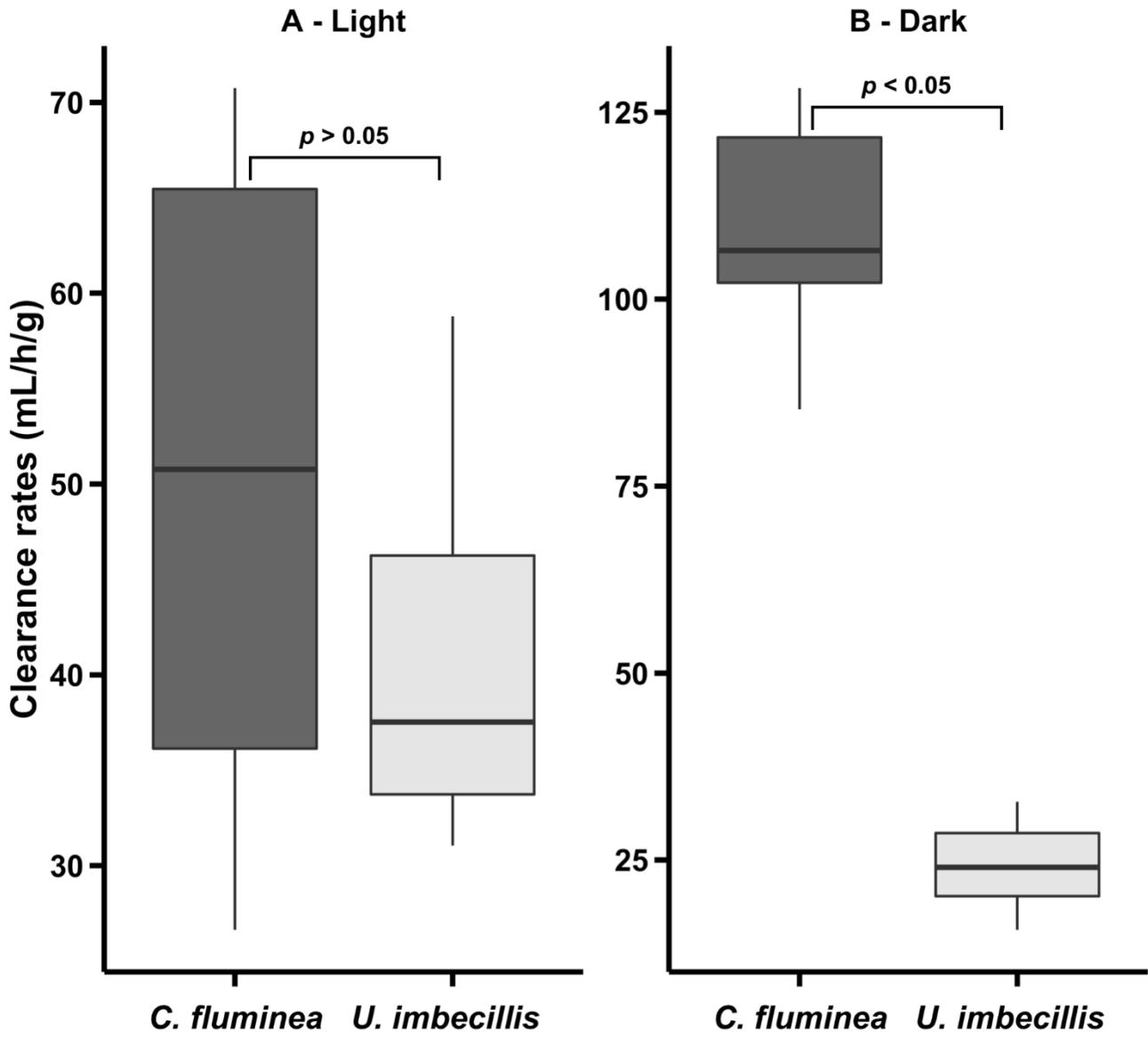


Fig. 1

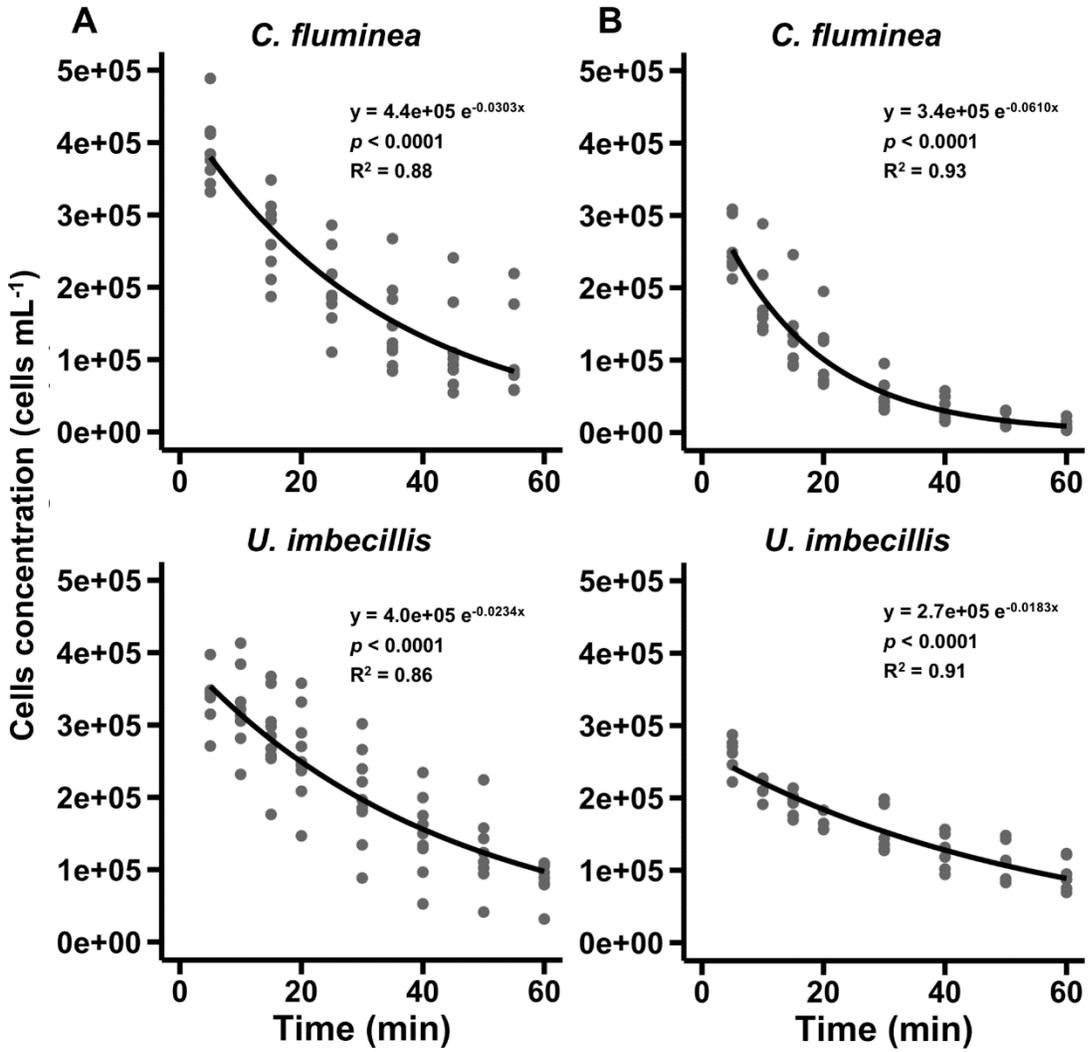


Fig. 2