

[Click here to view linked References](#)

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

3

4                                    Amber D. Hills<sup>a</sup>, Simon Pouil<sup>a</sup>, Dan Hua<sup>b</sup>, Teresa J. Mathews<sup>a</sup>

5

6                                    <sup>a</sup> Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37830, USA

7                                    <sup>b</sup> Cumberland River Aquatic Center, Tennessee Wildlife Resources Agency, Gallatin, TN 37066, USA

8

9                                    **Journal: Aquatic Ecology (Short Communication)**

10

11                                    \*Corresponding author: Teresa J. Mathews

12                                    Aquatic Ecology Group

13                                    Environmental Sciences Division

14                                    Oak Ridge National Laboratory

15                                    Oak Ridge, TN, 37830, USA

16                                    E-mail: [mathewstj@ornl.gov](mailto:mathewstj@ornl.gov)

17

18

19                                    **Acknowledgements**

20                                    This work was funded by the US Department of Energy's Oak Ridge Office of Environmental Management  
21                                    (ORO-DOE) and URS CH2M Oak Ridge LLC (UCOR) and is a product of ORNL's Mercury Remediation  
22                                    Technology Development Program. Special thanks to David Sims, Allison Fortner, Michael Jones, Trent  
23                                    Jett, and Nikki Jones for assistance with field collections of bivalves.

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

36 **Declarations**

37 **Funding**

38 This manuscript has been authored by UT-Battelle, LLC under Contract No. DE-AC05-00OR22725 with  
39 the U.S. Department of Energy. The United States Government retains and the publisher, by accepting the  
40 article for publication, acknowledges that the United States Government retains a non-exclusive, paid-up,  
41 irrevocable, worldwide license to publish or reproduce the published form of this manuscript, or allow  
42 others to do so, for United States Government purposes. The Department of Energy will provide public  
43 access to these results of federally sponsored research in accordance with the DOE Public Access Plan  
44 (<http://energy.gov/downloads/doe-public-access-plan>).

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<sup>-1</sup> h<sup>-1</sup> (Viergutz et al. 2012) while FRs in Unionidae usually  
76 ranges between 18 and 2000 mL ind<sup>-1</sup> h<sup>-1</sup> although FRs up to <10,000 mL mL ind<sup>-1</sup> h<sup>-1</sup> 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:  $3.50 \pm 0.35$  g wet wt, shell length:  
103  $20.2 \pm 0.9$  mm) were collected from Sewee Creek in Meigs county, TN, USA while *U. imbecillis* (weight:  
104  $21.2 \pm 8.2$  g wet wt, shell length:  $62.8 \pm 7.6$  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<sup>-1</sup>; ambient temperature: 14-28 °C; light intensity: 13-24 μmol m<sup>-2</sup> s<sup>-1</sup>; 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 10<sup>6</sup> cells g<sup>-1</sup> d<sup>-1</sup>) 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<sup>-2</sup> s<sup>-1</sup>; 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  $\mu\text{L}$  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 ( $\text{cells mL}^{-1}$ ) 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

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

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<sup>-1</sup> h<sup>-1</sup>) (see Marescaux et al. 2016 for review). The FRs in *U. imbecillis* (360-1169 mL ind<sup>-1</sup> h<sup>-1</sup>)  
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

## 210 **References**

211 Baker S. M., Hornbach D. J. (2001). Seasonal metabolism and biochemical composition of two unionid  
212 mussels, *Actinonaias ligamentina* and *Amblema plicata*. *Journal of Molluscan Studies*, 67, 407–416.  
213 <https://doi.org/DOI 10.1093/mollus/67.4.407>

214 Boltovskoy D., Izaguirre I., Correa N. (1995). Feeding selectivity of *Corbicula fluminea* (Bivalvia) on  
215 natural phytoplankton. *Hydrobiologia*. <https://doi.org/10.1007/BF00015510>

216 Duchini D., Boltovskoy D., Sylvester F. (2015). Detachment, displacement and reattachment activity in a  
217 freshwater byssate mussel (*Limnoperna fortunei*): the effects of light, temperature and substratum  
218 orientation. *Biofouling*, 31(7), 599–611. <https://doi.org/10.1080/08927014.2015.1080251>

219 Ferreira-Rodriguez N., Sousa R., Pardo I. (2018). Negative effects of *Corbicula fluminea* over native  
220 freshwater mussels. *Hydrobiologia*, 810(1), 85–95. <https://doi.org/10.1007/s10750-016-3059-1>

221 Gatenby C. M., Kreeger D. A., Patterson M. A., Marini M., Neves R. J. (2013). Clearance rates of *Villosa*  
222 *iris* (Bivalvia: Unionidae) fed different rations of the alga *Neochloris oleoabundans*. *Walkerana*, 16,  
223 9–20.

224 Gatenby C. M., Neves R. J., Parker B. C. (1996). Influence of sediment and algal food on cultured  
225 juvenile freshwater mussels. *Journal of the North American Benthological Society*, 15(4), 597–609.  
226 <https://doi.org/10.2307/1467810>

227 Geist J. (2010). Strategies for the conservation of endangered freshwater pearl mussels (*Margaritifera*  
228 *margaritifera* L.): a synthesis of Conservation Genetics and Ecology. *Hydrobiologia*, 644(1), 69–88.  
229 <https://doi.org/10.1007/s10750-010-0190-2>

230 Grutters B. M. C., Verhofstad M. J. J. M., van der Velde G., Rajagopal S., Leuven R. S. E. W. (2012). A  
231 comparative study of byssogenesis on zebra and quagga mussels: the effects of water temperature,

232 salinity and light-dark cycle. *Biofouling*, 28(2), 121–129.  
233 <https://doi.org/10.1080/08927014.2012.654779>

234 Haag W R, Warren M. L. (2000). Effects of light and presence of fish on lure display and larval release  
235 behaviours in two species of freshwater mussels. *Animal Behaviour*, 60, 879–886.  
236 [https://doi.org/DOI 10.1006/anbe.2000.1549](https://doi.org/DOI%2010.1006/anbe.2000.1549)

237 Haag, W. R., Williams, J. D. (2014). Biodiversity on the brink: an assessment of conservation strategies  
238 for North American freshwater mussels. *Hydrobiologia*, 735(1), 45–60.  
239 <https://doi.org/10.1007/s10750-013-1524-7>

240 Haag, W. R. (2012). North American freshwater mussels: Natural history, ecology, and conservation. In  
241 *North American Freshwater Mussels: Natural History, Ecology, and Conservation*.  
242 <https://doi.org/10.1017/CBO9781139048217>

243 Hansen B. W., Dolmer P., Vismann B. (2011). In situ method for measurements of community clearance  
244 rate on shallow water bivalve populations. *Limnology and Oceanography-Methods*, 9, 454–459.  
245 <https://doi.org/10.4319/lom.2011.9.454>

246 Hua D., Neves R. J., Jiao Y. (2013). Effects of algal density, water flow and substrate type on culturing  
247 juveniles of the rainbow mussel (*Villosa iris*) (Bivalvia: Unionidae) in a laboratory recirculating  
248 system. *Aquaculture*, 416, 367–373. <https://doi.org/10.1016/j.aquaculture.2013.09.002>

249 Kobak J., & Nowacki P. (2007). Light-related behaviour of the zebra mussel (*Dreissena polymorpha*,  
250 Bivalvia). *Fundamental and Applied Limnology*, 169(4), 341–352. [https://doi.org/10.1127/1863-](https://doi.org/10.1127/1863-9135/2007/0169-0341)  
251 [9135/2007/0169-0341](https://doi.org/10.1127/1863-9135/2007/0169-0341)

252 Loayza-Muro R., Elias-Letts R. (2007). Responses of the mussel *Anodontites trapesialis* (Unionidae) to  
253 environmental stressors: Effect of pH, temperature and metals on filtration rate. *Environmental*  
254 *Pollution*, 149(2), 209–215. <https://doi.org/10.1016/j.envpol.2007.01.003>

255 Marescaux J, Falisse E., Lorquet J., Van Doninck K., Beisel J. N., Descy J. P. (2016). Assessing filtration  
256 rates of exotic bivalves: dependence on algae concentration and seasonal factors. *Hydrobiologia*,  
257 *777*(1), 67–78. <https://doi.org/10.1007/s10750-016-2764-0>

258 Marescaux J., Falisse E., Lorquet J., Van Doninck K., Beisel J.-N., Descy J.-P. (2016). Assessing  
259 filtration rates of exotic bivalves: dependence on algae concentration and seasonal factors.  
260 *Hydrobiologia*, 777(1), 67–78. Retrieved from  
261 <https://link.springer.com/content/pdf/10.1007%2Fs10750-016-2764-0.pdf>

262 Mistry R., Ackerman J. D. (2017). Algal flux affects the clearance rates of recently metamorphosed  
263 freshwater mussels. *Aquatic Sciences*, 79(1), 139–148. <https://doi.org/10.1007/s00027-016-0485-0>

264 Mistry R., Ackerman J. D. (2018). Flow, Flux, and Feeding n Freshwater Mussels. *Water Resources*  
265 *Research*, 54(10), 7619–7630. <https://doi.org/10.1029/2018wr023112>

266 Morton B. (2008). The evolution of eyes in the Bivalvia: New insights. *American Malacological Bulletin*,  
267 26(1–2), 35–45. [https://doi.org/Doi 10.4003/006.026.0205](https://doi.org/Doi%2010.4003/006.026.0205)

268 Ortman C., Grieshaber M. K. (2003). Energy metabolism and valve closure behaviour in the Asian clam  
269 *Corbicula fluminea*. *Journal of Experimental Biology*, 206(22), 4167–4178. Retrieved from  
270 <http://jeb.biologists.org/content/jexbio/206/22/4167.full.pdf>

271 Otter R. R., McKinney D., Brown B., Lainer S., Monroe W., Hubbs D., Read B. (2015). Bioaccumulation  
272 of metals in three freshwater mussel species exposed in situ during and after dredging at a coal ash  
273 spill site (Tennessee Valley Authority Kingston Fossil Plant). *Environmental Monitoring and*  
274 *Assessment*, 187(6). [https://doi.org/ARTN 33410.1007/s10661-015-4578-3](https://doi.org/ARTN%2033410.1007/s10661-015-4578-3)

275 Pigneur L. M., Falisse E., Roland K., Everbecq E., Deliege J. F., Smitz J. S., ... Descy J. P. (2014).  
276 Impact of invasive Asian clams, *Corbicula* spp., on a large river ecosystem. *Freshwater Biology*,  
277 59(3), 573–583. <https://doi.org/10.1111/fwb.12286>

278 R Development Core Team. (2020). *R: A language and environment for statistical computing*. Vienna,  
279 Austria: R Foundation for Statistical Computing.

280 Riisgård H. U. (2001). On measurement of filtration rates in bivalves—the stony road to reliable data:  
281 review and interpretation. *MARINE ECOLOGY PROGRESS SERIES*, 211, 275–291.

282 Rosa I. C., Costa R., Goncalves F., Pereira J. L. (2014). Bioremediation of Metal-Rich Effluents: Could  
283 the Invasive Bivalve *Corbicula fluminea* Work as a Biofilter? *Journal of Environmental Quality*,

284 43(5), 1536–1545. <https://doi.org/10.2134/jeq2014.02.0069>

285 Salerno J., Gillis P. L., Bennett C. J., Sibley P. K., Prosser R. S. (2018). Investigation of clearance rate as  
286 an endpoint in toxicity testing with freshwater mussels (Unionidae). *Ecotoxicol Environ Saf*, 163,  
287 165–171. <https://doi.org/10.1016/j.ecoenv.2018.07.054>

288 Strayer D. L. (1999). Effects of alien species on freshwater mollusks in North America. *Journal of the*  
289 *North American Benthological Society*, 18(1), 74–98. <https://doi.org/10.2307/1468010>

290 Tankersley R A, Dimock R. V. (1993). The Effect of Larval Brooding on the Respiratory Physiology of  
291 the Fresh-Water Unionid Mussel Pyganodon-Cataracta. *American Midland Naturalist*, 130(1), 146–  
292 163. <https://doi.org/10.2307/2426283>

293 Tankersley R. A. (1996). Multipurpose gills: effect of larval brooding on the feeding physiology of  
294 freshwater unionid mussels. *Invertebrate Biology*, 243–255.

295 Tuttle-Raycraft S., Ackerman J. D. (2018). Does size matter? Particle size vs. quality in bivalve  
296 suspension feeding. *Freshwater Biology*, 63(12), 1560–1568. <https://doi.org/10.1111/fwb.13184>

297 Tuttle- Raycraft S., Ackerman J. D. (2019). Living the high turbidity life: The effects of total suspended  
298 solids, flow, and gill morphology on mussel feeding. *Limnology and Oceanography*.  
299 <https://doi.org/10.1002/lno.11202>

300 Vaughn C. C., Taylor C. M. (1999). Impoundments and the decline of freshwater mussels: A case study  
301 of an extinction gradient. *Conservation Biology*. <https://doi.org/10.1046/j.1523-1739.1999.97343.x>

302 Viergutz C., Linn C., Weitere M. (2012). Intra- and interannual variability surpasses direct temperature  
303 effects on the clearance rates of the invasive clam *Corbicula fluminea*. *Marine Biology*, 159(11),  
304 2379–2387. <https://doi.org/10.1007/s00227-012-1902-0>

305 Wilkens L. A. (2008). Primary inhibition by light: A unique property of bivalve photoreceptors. *American*  
306 *Malacological Bulletin*, 26(1–2), 101–109. <https://doi.org/10.4003/006.026.0210>

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 <sup>-1</sup> h <sup>-1</sup> )	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<sup>-1</sup> h<sup>-1</sup> 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 25<sup>th</sup> and 75<sup>th</sup> 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 <sup>1</sup>).

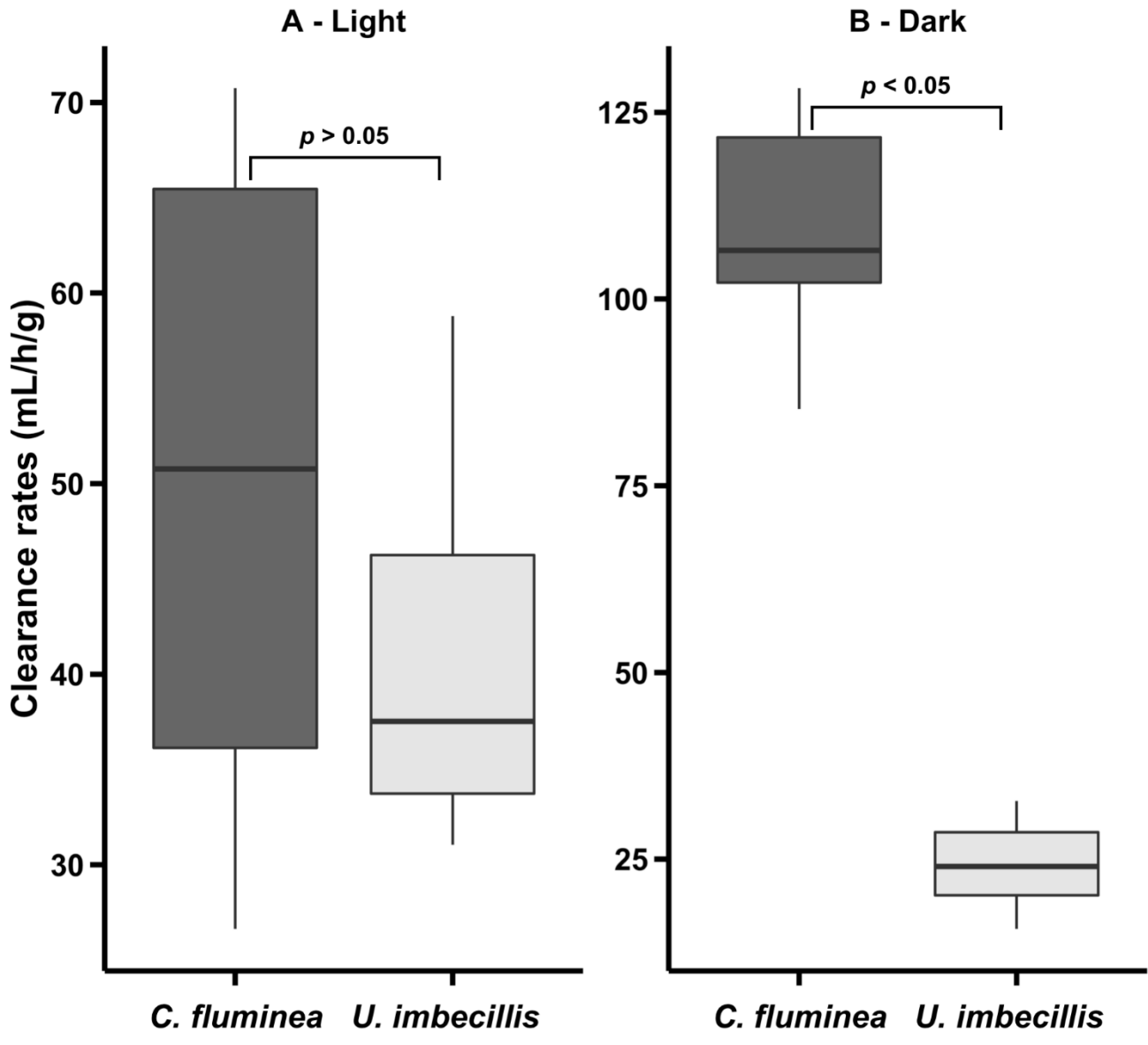


Fig. 1



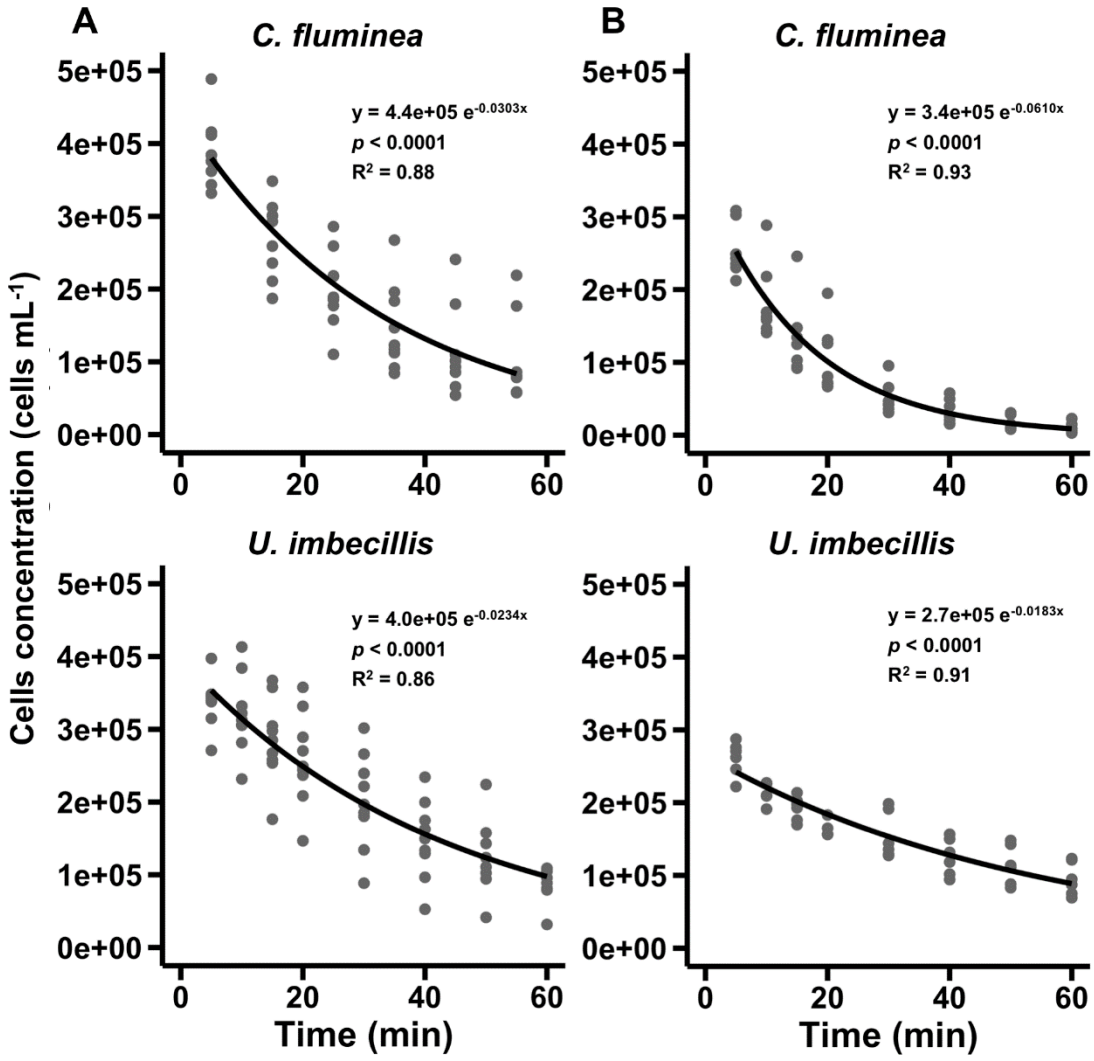


Fig. 2