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**Allometric relationships in the filtration rates of
the Asian clam *Corbicula fluminea* fed two phytoplankton species**

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15 **Abstract**

16 Filtration rates (FRs) of the invasive Asian clam *C. fluminea* of various sizes ranging from 0.5 to
17 4.5 g whole-body weight were experimentally assessed under controlled laboratory conditions
18 using two phytoplankton species of different sizes and biovolumes (*Chlamydomonas reinhardtii*
19 and *Pseudokirchneriella subcapitata*) as food. Overall, the FRs ranged from 0 to 347 mL g⁻¹ h⁻¹
20 (median value: 52 mL g⁻¹ h⁻¹). We found no statistical difference ($p > 0.05$) between the two
21 phytoplankton species used, nor did we find a significant relationship between individual FRs
22 (mL individual⁻¹ h⁻¹) and fresh weight (FW) or shell length (SL). However, we did find a
23 significant negative relationship between FRs (mL g⁻¹ h⁻¹) and FW in clams fed on *C. reinhardtii*
24 and *P. subcapitata* (FR = 131 FW^{-1.05} and FR = 203 FW^{-1.28}, respectively), indicating that smaller
25 (younger) individuals had a higher FR than larger (older) individuals in the tested range of
26 particle size (i.e. 4-6 μm diameter). Such results highlight the strong influence of size/age on the
27 filtration rate of *C. fluminea* and provide new insights to better understand the invasive capacity
28 of this species.

29 **Keywords:** Allometry, Filtration rate, Clearance rate, Asian clam

30 **1. Introduction**

31 The Asian clam *Corbicula fluminea* became invasive after deliberate introductions in Europe and
32 the Americas (Mouthon, 1981; McMahon, 1982; Kraemer and Galloway, 1986; Araujo et al.,
33 1993; Phels, 1994). As an active filter-feeder, this species removes suspended organic matter
34 from the water column and plays an important role in the transfer of nutrients and energy to the
35 sediment (Sousa et al., 2013; Higgins et al., 2014; Marescaux et al., 2016). Such changes in
36 nutrient dynamics may have significant consequences on freshwater ecosystems. For example,
37 the removal of algal particles by clam filtration lowers the turbidity, stimulating macrophyte
38 growth (Sousa et al., 2013) potentially inducing changes in food web structure and ecosystem
39 function. In addition to the indirect impacts of filter-feeder behavior of *C. fluminea* on ecosystem
40 function, invasion by Asian clams may have direct negative consequences on native bivalve
41 populations through competition for food resources (Ferreira-Rodríguez et al., 2018; Modesto et
42 al., 2019). For example, the high filtration capacities of *C. fluminea* (up to $> 3000 \text{ mL h}^{-1}$ per
43 individual, Viergutz et al., 2012, compared to $\sim 150\text{-}300 \text{ ml h}^{-1}$ per individual for similarly sized
44 native species, Mistry and Ackerman, 2018, Tuttle-Raycraft and Ackerman, 2018.) have been
45 put forward to explain the negative effects of Asian clams on other suspension feeder organisms
46 (Pigneur et al., 2014).

47 Assessing the factors influencing filtration rate (FR) in *C. fluminea* is important to better
48 understand the invasive capacity of this species and better predict the potential effects of Asian
49 clam invasion on freshwater ecosystems (Marescaux et al., 2016). A considerable amount of data
50 has been published on FRs of *Corbicula* species (see Marescaux et al., 2016 for review) showing
51 that FRs are affected by both abiotic and biotic factors. Among the abiotic factors, several
52 studies have shown that temperature plays an important role in determining FRs (Lauritsen,

53 1995; Lim et al., 2005; Pouil et al. 2021) and demonstrated that FRs may be affected by the
54 occurrence of contaminants (e.g. Oliveira et al., 2018). In addition, recent evidence shows that
55 light may affect FRs in *C. fluminea* (Hills et al., 2020; Pouil et al., 2021). Numerous studies have
56 also shown that biotic factors such as food availability and food type (Lauritsen, 1995; Lim et al.,
57 2005; Pouil et al., 2021), as well as reproduction and growth cycle (Viergutz et al., 2012) can
58 also influence FRs.

59 Physiological processes and morphological structures in bivalves are related to the size of the
60 individual. The scaling of biological variables such as filtration with increasing size can be
61 described by power functions (Møhlenberg and Riisgård, 1979). Many studies have
62 demonstrated allometric relationships between individual FR and size, particularly in marine
63 bivalves. For example, experimental studies have found that the FR of an individual is almost
64 proportional to the square of its shell length (SL) in the blue mussel *Mytilus edulis* (i.e. $FR \approx$
65 SL^2 ; Jones et al., 1992; Riisgård, 2001; Riisgård et al., 2011) while individual FR is also a
66 function of the body dry weight (DW) in the same species ($FR \approx DW^{2/3}$; Riisgård et al., 2014). A
67 meta-analysis performed by Cranford et al. (2011) showed that such relationships are relatively
68 constant in 21 marine bivalve species even if results may slightly differ among species and
69 studies. Overall, less information is available for freshwater bivalves and surprisingly, while
70 there is data in the literature on FRs for *C. fluminea* (Marescaux et al., 2016), the effects of
71 size/weight on FRs have been poorly investigated in this species.

72 Allometric equations for FRs of bivalves are widely used in physiological, ecological, and
73 modelling studies (e.g. Cranford et al., 2011), and therefore, it is important to define these
74 equations in *C. fluminea*. In the present laboratory study, we investigated the FR of *C. fluminea*
75 ranging in size from 0.5 to 4.5 g whole-body fresh weight using two different phytoplankton

76 species of two different sizes and biovolumes (*Chlamydomonas reinhardtii* and
77 *Pseudokirchneriella subcapitata*). Our results are therefore relevant to the broader evaluation of
78 FRs in *C. fluminea* and contribute to a better understanding of this species' invasion capabilities.

79

80 **2. Materials and Methods**

81 2.1. Origin and acclimation of *C. fluminea*

82 Adult *C. fluminea* were collected from Sewee Creek in Meigs county, TN, USA
83 (35°33'52.254N, 84°47'53.487W). Clams were brought to the laboratory in a cooler with an air
84 bubbler. No mortality was recorded during transportation. The bivalves were kept in a 150-L
85 tank supplied with flow-through water from First Creek on the Oak Ridge Reservation in Oak
86 Ridge, TN (water renewal: 300 L h⁻¹; ambient temperature: 15-20°C; light/dark: 12h/12h), and
87 acclimated to the laboratory for at least six months prior to the experiment. In addition to the
88 supply of food particles coming from the water inlet (i.e. ~1,000 particles mL⁻¹), bivalves were
89 fed a daily diet of fresh algae: *C. reinhardtii* and *P. subcapitata* (ex *Raphidocelis subcapitata*)
90 (approx. 8 x 10⁷ cells ind⁻¹ d⁻¹) using a peristaltic pump. The effects of size on the filtration rates
91 of *C. fluminea* were assessed through the measurements of the volume of water cleared of
92 suspended particles per unit of time (i.e. 'clearance method'; Riisgård, 2001).

93

94 2.2. Algae culture

95 In our experiments, we used two species of chlorophytes of differing cell size to assess FRs in *C.*
96 *fluminea*, *C. reinhardtii* (5-6 µm in equivalent spherical diameter [ESD] and average of 78 µm³

97 in volume ESD) and *P. subcapitata* (average: 4-5 μm and average of 56 μm^3 in volume ESD).
98 Previous work has shown that phytoplankton cell size may affect the FR of bivalves (e.g.
99 Strohmeier et al., 2012). Furthermore, these species remain in suspension, facilitating the
100 homogeneity of the particles required to properly estimate FRs.

101 Algae were grown as described by Pouil et al. (2021). Briefly, phytoplankton were grown in 10-
102 L clear Nalgene carboys containing WC medium (Guillard, 1975) (temperature: 23-24 $^{\circ}\text{C}$; light
103 intensity: 150-200 $\mu\text{mol m}^{-2} \text{s}^{-1}$; light/dark: 12h/12h). Cell cultures were used during their
104 exponential growth phase. Cells were concentrated by centrifuge (5000 RPM for 5 min) and cell
105 densities were verified by flow imaging cytometry as described in Section 2.4.

106

107 2.3. Filtration rate experiment

108 To assess the effects of size on the filtration of *C. fluminea*, an allometry experiment was
109 performed where FRs were assessed using both *C. reinhardtii* and *P. subcapitata* at a
110 concentration of 100,000 cells mL^{-1} . Prior to the experiment, individuals of *C. fluminea* ($n = 100$,
111 0.36-4.83 g wet wt, 8.7-20.8 mm shell length) were carefully dried of excess moisture and
112 weighed using a microbalance (accuracy: ± 0.1 mg) and shell length and width were measured
113 using a digital caliper (accuracy: ± 0.2 mm). Each individual was randomly selected and placed
114 in a food-grade PET container filled with 200 mL of 75- μm filtered stream water (< 1000
115 particles mL^{-1} , T°C : 19.6 $^{\circ}\text{C}$, pH: 7.8, conductivity: 310 $\mu\text{S cm}^{-1}$, alkalinity and hardness; 162 mg
116 $\text{CaCO}_3 \text{ L}^{-1}$, O_2 : 5.97 mg L^{-1} , NH_4^+ : 0.02 mg L^{-1} , NO_2^- : 0.002 mg L^{-1} , NO_3^- : 0.196 mg L^{-1}) with
117 air bubbling keeping the water well-circulated. Clams were acclimated to experimental
118 containers for 4 h at a light intensity of 10-12 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Depending on their weight, each clam

119 was assigned to an experimental treatment (i.e. one of two algal species used) to get a
120 comparable size range between the two species of algae used (n = 50 clams per treatment).

121 At the start of the experiment, concentrated live algae cells were pipetted into each PET
122 container filled with filtered stream water to add the targeted initial concentration as previously
123 described (Hills et al., 2020; Pouil et al., 2021). The initial cell concentration was immediately
124 verified by analyzing 4-mL samples from each of the three control containers using flow imaging
125 cytometry (see Section 2.4). The actual initial concentrations were $102,491 \pm 4,715$ and $107,270$
126 $\pm 1,101$ cells mL⁻¹ for *C. reinhardtii* and *P. subcapitata*, respectively. A 4-mL sample was taken
127 from each plastic container 10 minutes after the algae addition and then a second 4-mL sample at
128 the end of the 40-minute filtration period. Samples were placed in 5-mL snap-cap centrifuge
129 tubes containing 800 µL of 10% formalin solution, a common preservative for phytoplankton
130 samples (Mukherjee et al., 2014) and mixed immediately.

131

132 2.4. Algal cell counts

133 Algal cell counts were performed by flow imaging cytometry (FlowCam® Benchtop B3 Model)
134 following a standard procedure (Zarauz and Irigoien, 2008; Pouil et al., 2021) within a week of
135 sampling to limit the effect of preservative. The preserved samples were analyzed in AutoImage
136 mode in which the sample is pumped across a flow cell and particles are imaged at regular
137 intervals. Therefore, every particle (phytoplankton, aggregates, inorganic suspended solids, and
138 others) ranging from 2 to 10 µm ESD was counted and imaged. For each sample, a maximum of
139 either 10,000 particles or 1 mL were analyzed. A 10X objective and a 100-µm counting cell were
140 used in the sample analysis, and the instrument count-calibration was checked using beads of a

141 known size (Zarauz and Irigoien, 2008). Invalid pictures (i.e. bubbles, repeated images) were
142 removed from the image database through visual recognition. Each sample was run in duplicate
143 and mean values were then used for FR calculations.

144

145 2.5. Data treatment

146 Several clams were excluded from the analysis due to ruptured algal cells occurring in some PET
147 containers (n = 3 and n = 18 for clams fed on *C. reinhardtii* and *P. subcapitata*, respectively).

148 We believe that the ruptured cells were caused by excessive aeration in these containers.

149 The allometric relationship between gill surface area (SA, mm²) and shell length (SL, mm) for *C.*
150 *fluminea* can be approximately described by a linear relationship based on a regression model
151 described in Equation 1:

$$152 \quad (1) \text{ SA} = a + b \text{ SL}^2$$

153 With $a = 63.2 \pm 9$ and $b = 0.78 \pm 0.16$ as determined by Payne and Miller (1995).

154 FRs (expressed as mL g FW⁻¹ h⁻¹) were calculated in two ways, using whole body wet weight
155 and soft tissue wet weight, according to the equation modified from Coughlan (1969) (see Mistry
156 and Ackerman, 2018; Pouil et al., 2021):

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

157 where V is the volume of water in the PET container (mL), n is the number of individuals per
158 container (n=1), t is the length of the experiment (h), C_i and C_f are initial and final cell
159 concentrations respectively in the container with bivalves while, and C'_i and C'_f are average

160 initial and final cell concentrations respectively in the containers used as controls (with no
161 bivalve). Based on calculations, all the individuals with $FR < 1 \text{ mL g}^{-1} \text{ h}^{-1}$ were considered as
162 non-filtering

163 and excluded in the allometry relationship analysis (Pouil et al., 2021). FRs were then plotted
164 against individual whole-body or soft tissue weight wet (WW, g) and shell length (SL, mm) and
165 allometric relationships were tested using power models (Equation 2):

$$166 \quad (2) \text{ FR} = a * \text{WW}^b \text{ and } a * \text{SL}^b$$

167 Model constants were estimated by iterative adjustment using the least squares regression
168 method. To statistically assess the effect of food species on the FRs of *C. fluminea*, growth data
169 and FR values were linearized with a natural logarithmic transformation and an ANCOVA was
170 then applied to identify differences between the regression slopes. The level of significance for
171 statistical analyses was always set to $\alpha = 0.05$. All statistics were performed using R freeware
172 version 3.6.3 (R Development Core Team, 2020).

173

174 **3. Results and Discussion**

175 The FR experiment was performed using an initial algal cell concentration of $100,000 \text{ cells mL}^{-1}$
176 using two phytoplankton species (*C. reinhardtii* and *P. subcapitata*). Combining the two species,
177 and across all sizes of *C. fluminea*, FRs for *C. fluminea* ($n = 17-30$) ranged from 0 to 347 mL g^{-1}
178 h^{-1} (median value: $52 \text{ mL g}^{-1} \text{ h}^{-1}$) or 0 to $478 \text{ mL ind}^{-1} \text{ h}^{-1}$. While the highest FR values were
179 observed in clams fed on *P. subcapitata*, no statistical difference in FR was found between the
180 two experimental food types across all clam sizes ($t = 1.430$, $df = 22.77$, $p = 0.1636$, Figure 1A)

181 and the proportion of non-filtering individuals during this experiment remained similar for clams
182 fed on *P. subcapitata* and *C. reinhardtii* with 53% and 60%, respectively (Figure 1B).

183 Overall, our results are in the range of FRs previously reported. In their review, Marescaux et al.
184 (2016) reported FR values ranging from 29 mL ind⁻¹ h⁻¹ (Boltovskoy et al., 1995) to 3,252 mL
185 ind⁻¹ h⁻¹ (Viergutz et al., 2012) in *C. fluminea* suggesting a high plasticity in filtration in this
186 species. This wide range of FRs reported in the literature may be the result from various
187 environmental factors, as well from differences of experimental design of the filtration assays
188 (Marescaux et al., 2016). Interestingly, we found that some of the Asian clams did not filter
189 during the experiment and the proportion of non-filtering individuals remained similar to the
190 ones reported by Pouil et al. (2021) under similar experimental conditions (i.e. T: 20 °C, food: *C.*
191 *reinhardtii* at 100,000 cells mL⁻¹). In the present study we found that the non-filtering behavior
192 may be related to the size of the clams, as we found a slightly different distribution of sizes
193 between filtering and non-filtering individuals in which larger individuals were more likely to be
194 non-filtering (Figure 2), but this finding needs to be confirmed through further investigation.

195 Filtration rates for both phytoplankton species were inversely related to clam shell size, soft body
196 weight, and whole-body fresh weight in *C. fluminea* indicating that smaller (younger) individuals
197 had higher FRs than larger (older) individuals in the tested range of particle size (i.e. 4-6 µm
198 diameter ESD; Table 1; Figure 2). When significant, these allometric relationships were
199 described by a power function (Eq. 2). Lauritsen (1986) performed one of the first field studies
200 highlighting that FR on a per individual basis (mL ind⁻¹ h⁻¹) increased with individual size in *C.*
201 *fluminea* and found correlations between FR and SL (FR = 3.534 SL^{1.72}). Such results are
202 consistent with Cranford et al. (2011) who found from their meta-analysis that b-values of 1.78 ±
203 0.34 are generally applicable in allometric relationships between FR and SL in marine bivalve

204 species. However, we did not find a significant relationship between individual-based FRs (mL
205 ind⁻¹ h⁻¹) and FW or SL in our study. Other studies have also shown a lack of relationship
206 between individual based FRs and freshwater bivalve size (Sylvester et al., 2005; Pestana et al.,
207 2009), especially when there is considerable variability in FRs among individuals, even within
208 each size class, as in our study.

209 We found that FRs (mL g⁻¹ h⁻¹) decreased with increasing whole-body weight. Bivalve FRs can
210 vary in proportion to gill surface area (Meyhofer, 1985; Lei et al., 1996; Silverman et al., 1997).
211 In the present study, we estimated that the gill surface per unit of weight decreased when whole-
212 body weight increased (Figure 3) (Eq. 1; Payne and Miller 1995). This means that smaller
213 individuals have a larger gill surface area relative to their size. In addition, Ortmann and
214 Grieshaber (2003) found that larger (older) organisms are able to maintain lower metabolic rates
215 by closing their valves for hours and our results corroborate their findings with higher proportion
216 of larger individuals non-filtering (Figure 2C). Altogether, these findings can explain the
217 allometric relationships observed in the present study and corroborate previous literature data on
218 other species. Indeed, Sylvester et al. (2005) also found that smaller individuals of the golden
219 mussels *Limnoperna fortune* filtered more water per unit time than larger individuals and
220 assumed that this relationship is due to the decrease of gill surface to body size ratio, and to the
221 higher metabolic demands of younger specimens.

222 Allometric relationships in FRs of *C. fluminea* fed on the two phytoplankton species were not
223 significantly different ($F_{(1,44)} = 0.315$, $p = 0.577$) ($a = 130.92 \pm 13.02$ and $b = -1.05 \pm 0.16$ for *C.*
224 *reinhardtii* and $a = 203.07 \pm 32.71$ and $b = -1.28 \pm 0.35$ for *P. subcapitata*), although the size of
225 the individual algal cells varied by 150% in volume (*C. reinhardtii* is larger). Thus, although the
226 average FRs did not change with the two algal species used, at a concentration of 100,000 cells

227 mL⁻¹, the average volume of ingested cells in 40 min was 1.1 µL per individual for clam fed on
228 *C. reinhardtii* while this value reached 0.7 µL per individual in clams fed on *P. subcapitata*
229 showing that the clams feeding on the larger cells may be getting more carbon and other
230 nutrients. Some studies performed on other bivalve species have shown that small differences in
231 particle size may strongly affect their selection and retention by the bivalve and thus affect the
232 determination of FR. For example, Jacobs et al. (2015) found that the average retention in the
233 blue mussel *Mytilus edulis* is much higher for picophytoplankton (0.7–1.0 µm) compared to
234 bacteria (0.6 µm). In the present study, the absence of difference in FRs as well as the absence of
235 pseudo-feces, or rejected food, in our experiments suggest that the cells were indifferently
236 selected both by juvenile and adult clams. Our results corroborate previous studies showing that
237 *Corbicula* species are able to feed on smaller particles than most native freshwater bivalves such
238 as Unionidae and Sphaeriidae (see Marescaux et al., 2006). Way et al. (1990), in an experimental
239 study, also shown that filtration rates of *C. fluminea* were highest with the smallest natural
240 suspended particles they used (i.e. 3 x 5 µm).

241 This study highlights the importance of taking into account the effects of size on FR in *C.*
242 *fluminea* to better understand the impacts of this species on freshwater ecosystems, in particular
243 the flow of nutrients generated by filtration activity. *C. fluminea*'s ability to filter faster as a
244 smaller individual may be part of the species' suite of r-selected species traits that enable it to
245 successfully invade novel habitats by allowing faster colonization and population establishment.
246 Indeed, the species has higher filtration and assimilation rates than other freshwater bivalve
247 species which adapt it for life in unstable environments (McMahon 2002). Exotic *C. fluminea*
248 can be less sensitive to contaminants than native bivalve species as shown for example for
249 mercury (Oliveira et al., 2015) and thus maintain populations in degraded streams where other

250 bivalve species disappear. Through the continuous filtration of water and its benthic lifestyle,
251 Asian clams can strongly accumulate certain compounds including both organic (Colombo et al.,
252 1995; Jacomini et al., 2006) and inorganic (Bonnail et al., 2016) contaminants. Several programs
253 have thus been carried out to evaluate the potential use of *C. fluminea* as a bioindicator species
254 (e.g. Sherman et al., 2009) and even its use in bioremediation (Rosa et al., 2014), requiring a
255 better understanding of the factors influencing their FR. Our findings also help to refine the
256 potential use of this species in biomonitoring and/or bioremediation programs for contamination.

257

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389 **Figure captions**

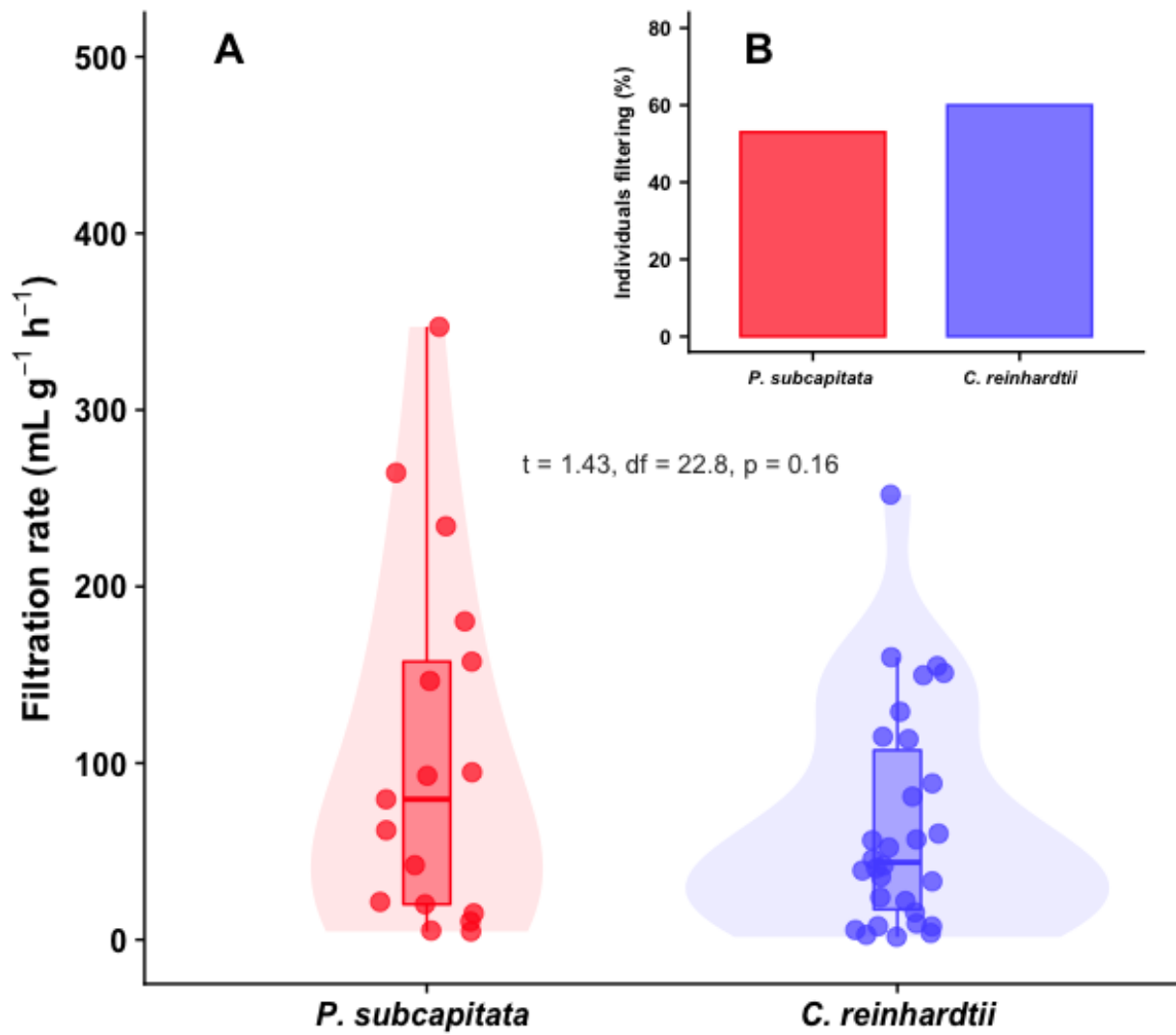
390 **Figure 1.** (A) Filtration rates (FRs; expressed as mL g fresh weight⁻¹ h⁻¹) of *Corbicula fluminea*
391 (n = 17-30) fed on two phytoplankton species (*Chlamydomonas reinhardtii* and
392 *Pseudokirchneriella subcapitata*) and (B) percent of individuals filtering during the experiment
393 for the two food conditions. Dots are the individual data, whiskers indicate the minimum and
394 maximum values, lines the median, boxes represent 25th and 75th percentiles and shading areas
395 show the probability density of the data at different values.

396

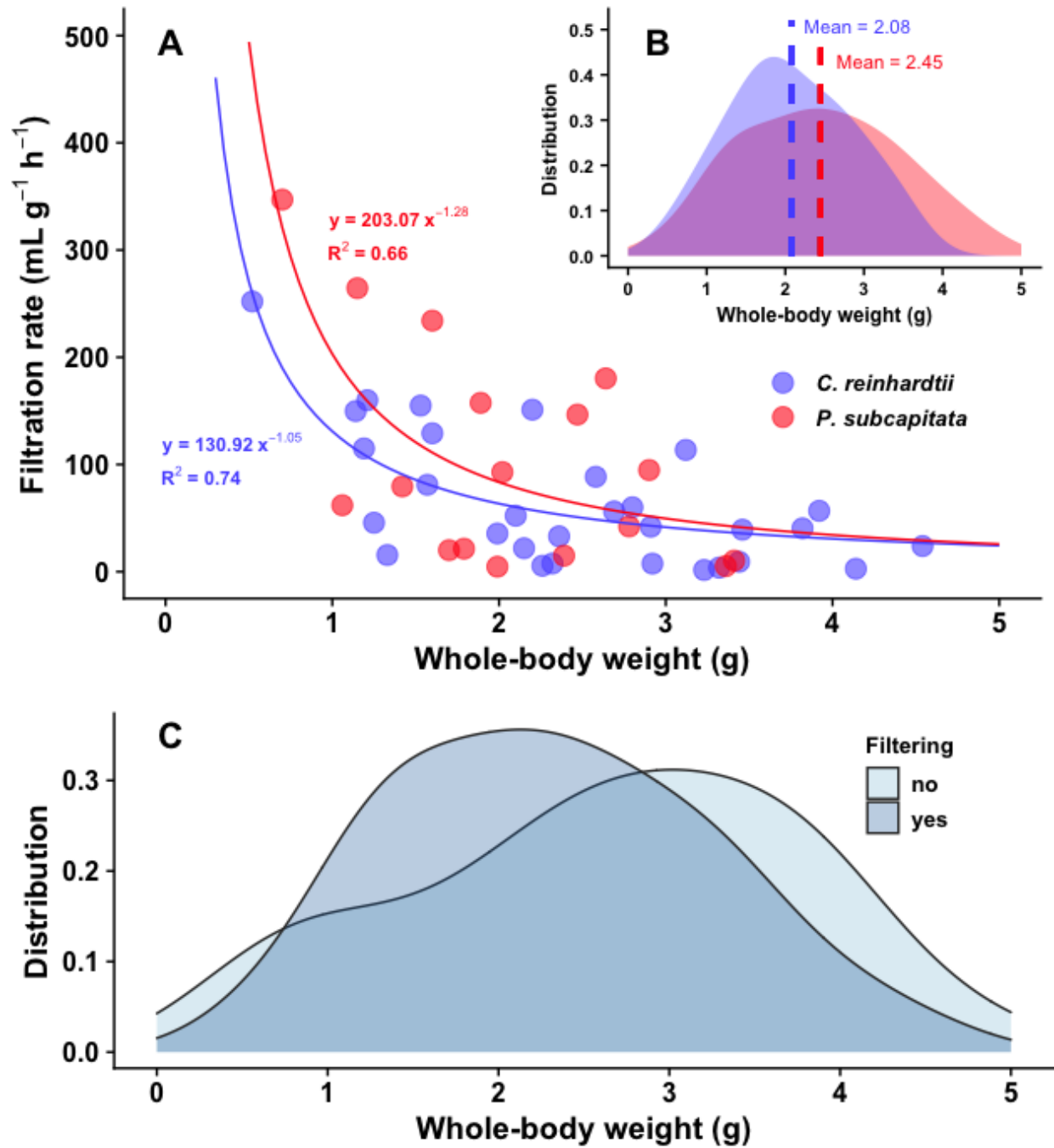
397 **Figure 2.** (A) Relationships between FR and whole-body wet weight (g) in *Corbicula fluminea*
398 fed on two phytoplankton species (i.e. *Chlamydomonas reinhardtii* and *Pseudokirchneriella*
399 *subcapitata*), (B) distribution in size for each food condition and (C) among the non-filtering and
400 filtering individuals. Details of model fitting are given in Table 1.

401

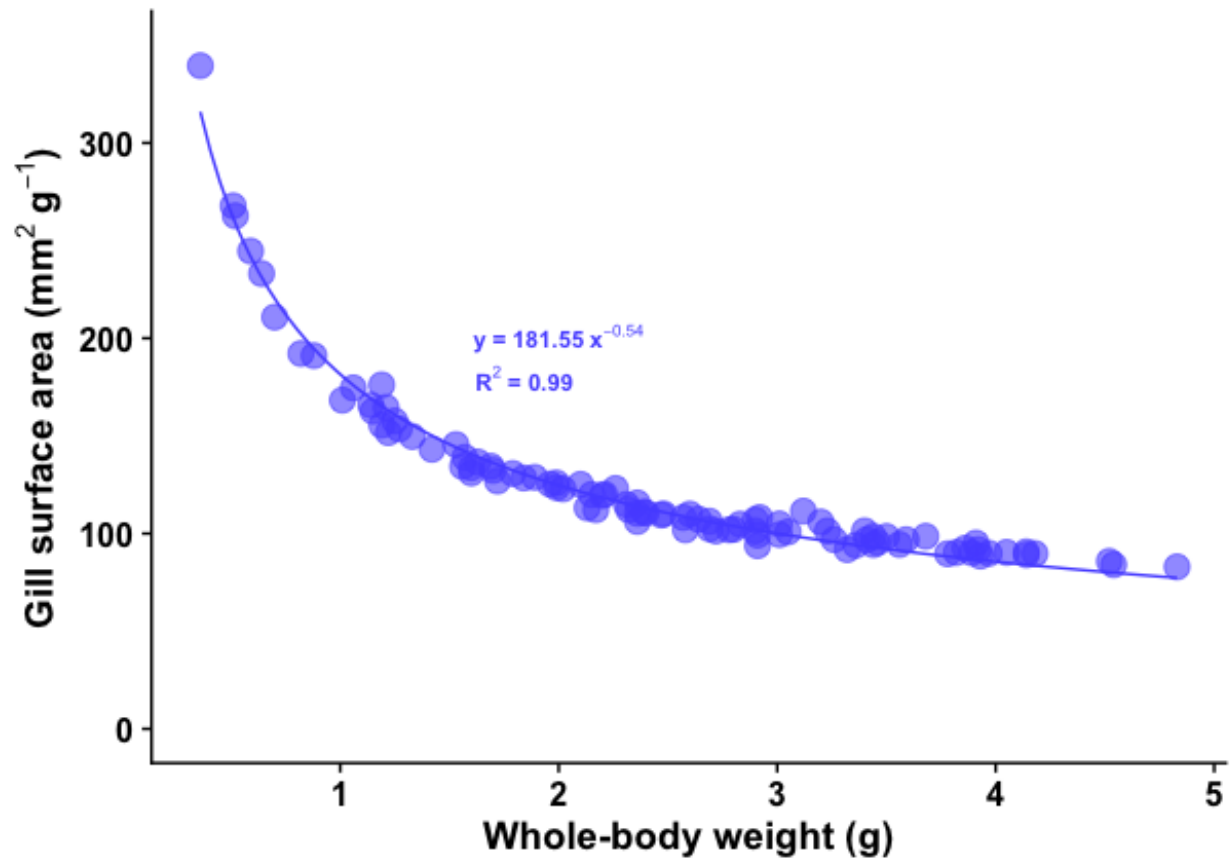
402 **Figure 3.** Relationship between whole-body fresh (g) of *C. fluminea* and the gill surface area per
403 unit of weight (mm² g⁻¹) estimated from Payne and Miller (1995) equation.



404 Figure 1



405 Figure 2



406 Figure 3

407 Table 1. Parameters and statistics of the power function best describing the relationships
 408 between FRs of *C. fluminea* fed on *C. reinhardtii* and *P. subcapitata* and body size (i.e. whole-

Food	a (Mean ± SE)	p(a)	b (Mean ± SE)	p(b)	R ²
Whole-body weight (g)					
<i>C. reinhardtii</i>	130.92 ± 13.02	< 0.0001	-1.05 ± 0.16	< 0.0001	0.74
<i>P. subcapitata</i>	203.07 ± 32.71	< 0.0001	-1.28 ± 0.35	0.0002	0.66
Soft tissues weight (g)					
<i>C. reinhardtii</i>	5.91 ± 3.03	0.0611	-1.3 ± 0.23	< 0.0001	0.74
<i>P. subcapitata</i>	7.13 ± 8.59	0.4197	-1.46 ± 0.56	0.0209	0.57
Shell length (mm)					
<i>C. reinhardtii</i>	2.53 10 ⁵ ± 2.97 10 ⁵	0.402	-3.03 ± 0.46	< 0.0001	0.72
<i>P. subcapitata</i>	1.65 10 ⁶ ± 3.74 10 ⁶	0.66577	-3.63 ± 0.90	0.0011	0.68

409 body and soft tissues weights and shell length) of the clams (n= 17-30).