

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

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Simon Pouil, Amber Hills, Louise Stevenson, Teresa Mathews. Allometric relationships in the filtration rates of the Asian clam Corbicula fluminea fed two phytoplankton species. Aquatic Ecology, 2021, 55 (3), pp.915-923. 10.1007/s10452-021-09871-4 . hal-03364999

## HAL Id: hal-03364999 https://hal.science/hal-03364999

Submitted on 5 Sep 2023

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

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 from the water column and plays an important role in the transfer of nutrients and energy to the 34 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, the removal of algal particles by clam filtration lowers the turbidity, stimulating macrophyte 37 38 growth (Sousa et al., 2013) potentially inducing changes in food web structure and ecosystem function. In addition to the indirect impacts of filter-feeder behavior of C. fluminea on ecosystem 39 function, invasion by Asian clams may have direct negative consequences on native bivalve 40 populations through competition for food resources (Ferreira-Rodríguez et al., 2018; Modesto et 41 al., 2019). For example, the high filtration capacities of C. fluminea (up to > 3000 mL h<sup>-1</sup> per 42 individual, Viergutz et al., 2012, compared to  $\sim$ 150-300 ml h<sup>-1</sup> per individual for similarly sized 43 native species, Mistry and Ackerman, 2018, Tuttle-Raycraft and Ackerman, 2018.) have been 44 put forward to explain the negative effects of Asian clams on other suspension feeder organisms 45 46 (Pigneur et al., 2014).

Assessing the factors influencing filtration rate (FR) in *C. fluminea* is important to better understand the invasive capacity of this species and better predict the potential effects of Asian clam invasion on freshwater ecosystems (Marescaux et al., 2016). A considerable amount of data has been published on FRs of *Corbicula* species (see Marescaux et al., 2016 for review) showing that FRs are affected by both abiotic and biotic factors. Among the abiotic factors, several 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 individual. The scaling of biological variables such as filtration with increasing size can be 60 61 described by power functions (Møhlenberg and Riisgård, 1979). Many studies have demonstrated allometric relationships between individual FR and size, particularly in marine 62 bivalves. For example, experimental studies have found that the FR of an individual is almost 63 proportional to the square of its shell length (SL) in the blue mussel Mytilus edulis (i.e. FR  $\approx$ 64 SL<sup>2</sup>; Jones et al., 1992; Riisgård, 2001; Riisgård et al., 2011) while individual FR is also a 65 function of the body dry weight (DW) in the same species (FR  $\approx$  DW<sup>2/3</sup>; Riisgård et al., 2014). A 66 meta-analysis performed by Cranford et al. (2011) showed that such relationships are relatively 67 constant in 21 marine bivalve species even if results may slightly differ among species and 68 studies. Overall, less information is available for freshwater bivalves and surprisingly, while 69 there is data in the literature on FRs for C. fluminea (Marescaux et al., 2016), the effects of 70 size/weight on FRs have been poorly investigated in this species. 71

Allometric equations for FRs of bivalves are widely used in physiological, ecological, and modelling studies (e.g. Cranford et al., 2011), and therefore, it is important to define these equations in *C. fluminea*. In the present laboratory study, we investigated the FR of *C. fluminea* ranging in size from 0.5 to 4.5 g whole-body fresh weight using two different phytoplankton species of two different sizes and biovolumes (*Chlamydomonas reinhardtii* and *Pseudokirchneriella subcapitata*). Our results are therefore relevant to the broader evaluation of
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*

Adult C. fluminea were collected from Sewee Creek in Meigs county, TN, USA 82 83 (35°33'52.254N, 84°47'53.487W). Clams were brought to the laboratory in a cooler with an air bubbler. No mortality was recorded during transportation. The bivalves were kept in a 150-L 84 tank supplied with flow-through water from First Creek on the Oak Ridge Reservation in Oak 85 Ridge, TN (water renewal: 300 L h<sup>-1</sup>; ambient temperature: 15-20°C; light/dark: 12h/12h), and 86 acclimated to the laboratory for at least six months prior to the experiment. In addition to the 87 supply of food particles coming from the water inlet (i.e.  $\sim 1.000$  particles mL<sup>-1</sup>), bivalves were 88 fed a daily diet of fresh algae: C. reinhardtii and P. subcapitata (ex Raphidocelis subcapitata) 89 (approx. 8 x  $10^7$  cells ind<sup>-1</sup> d<sup>-1</sup>) using a peristaltic pump. The effects of size on the filtration rates 90 of C. fluminea were assessed through the measurements of the volume of water cleared of 91 suspended particles per unit of time (i.e. 'clearance method'; Riisgård, 2001). 92

93

94 2.2. Algae culture

In our experiments, we used two species of chlorophytes of differing cell size to assess FRs in *C*.
 *fluminea*, *C. reinhardtii* (5-6 µm in equivalent spherical diameter [ESD] and average of 78 µm<sup>3</sup>

97 in volume ESD) and *P. subcapitata* (average: 4-5  $\mu$ m and average of 56  $\mu$ m<sup>3</sup> 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 °C; light 103 intensity: 150-200  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>; 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 performed where FRs were assessed using both C. reinhardtii and P. subcapitata at a 109 concentration of 100,000 cells mL<sup>-1</sup>. Prior to the experiment, individuals of C. fluminea (n = 100, 110 0.36-4.83 g wet wt, 8.7-20.8 mm shell length) were carefully dried of excess moisture and 111 weighed using a microbalance (accuracy:  $\pm 0.1$  mg) and shell length and width were measured 112 113 using a digital caliper (accuracy:  $\pm 0.2$  mm). Each individual was randomly selected and placed in a food-grade PET container filled with 200 mL of 75-µm filtered stream water (< 1000 114 particles mL<sup>-1</sup>, T°C: 19.6°C, pH: 7.8, conductivity: 310 µS cm<sup>-1</sup>, alkalinity and hardness; 162 mg 115 CaCO<sub>3</sub> L<sup>-1</sup>, O<sub>2</sub>: 5.97 mg L<sup>-1</sup>, NH<sub>4</sub><sup>+</sup>: 0.02 mg L<sup>-1</sup>, NO<sub>2</sub><sup>-</sup>: 0.002 mg L<sup>-1</sup>, NO<sub>3</sub><sup>-</sup>: 0.196 mg L<sup>-1</sup>) with 116 air bubbling keeping the water well-circulated. Clams were acclimated to experimental 117 containers for 4 h at a light intensity of 10-12  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>. Depending on their weight, each clam 118

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 $\pm$  1,101 cells mL<sup>-1</sup> for *C. reinhardtii* and *P. subcapitata*, respectively. A 4-mL sample was taken 126 127 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 tubes containing 800 µL of 10% formalin solution, a common preservative for phytoplankton 129 samples (Mukherjee et al., 2014) and mixed immediately. 130

131

#### 132 2.4. Algal cell counts

Algal cell counts were performed by flow imaging cytometry (FlowCam® Benchtop B3 Model) 133 134 following a standard procedure (Zarauz and Irigoien, 2008; Pouil et al., 2021) within a week of sampling to limit the effect of preservative. The preserved samples were analyzed in AutoImage 135 mode in which the sample is pumped across a flow cell and particles are imaged at regular 136 137 intervals. Therefore, every particle (phytoplankton, aggregates, inorganic suspended solids, and others) ranging from 2 to 10 µm ESD was counted and imaged. For each sample, a maximum of 138 139 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 known size (Zarauz and Irigoien, 2008). Invalid pictures (i.e. bubbles, repeated images) were
removed from the image database through visual recognition. Each sample was run in duplicate
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,  $mm^2$ ) and shell length (SL, mm) for C.

*fluminea* can be approximately described by a linear relationship based on a regression modeldescribed in Equation 1:

152 (1)  $SA = a + b SL^2$ 

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

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

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

where V is the volume of water in the PET container (mL), n is the number of individuals per container (n=1), t is the length of the experiment (h),  $C_i$  and  $C_f$  are initial and final cell concentrations respectively in the container with bivalves while, and C'<sub>i</sub> and C'<sub>f</sub> are average initial and final cell concentrations respectively in the containers used as controls (with no bivalve). Based on calculations, all the individuals with  $FR < 1 \text{ mL g}^{-1} \text{ h}^{-1}$  were considered as non-filtering

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

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

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

173

#### 174 **3. Results and Discussion**

The FR experiment was performed using an initial algal cell concentration of 100,000 cells mL<sup>-1</sup> using two phytoplankton species (*C. reinhardtii* and *P. subcapitata*). Combining the two species, and across all sizes of *C. fluminea*, FRs for *C. fluminea* (n = 17-30) ranged from 0 to 347 mL g<sup>-1</sup> h<sup>-1</sup> (median value: 52 mL g<sup>-1</sup> h<sup>-1</sup>) or 0 to 478 mL ind<sup>-1</sup> h<sup>-1</sup>. While the highest FR values were observed in clams fed on *P. subcapitata*, no statistical difference in FR was found between the two experimental food types across all clam sizes (t = 1.430, df = 22.77, p = 0.1636, Figure 1A) 182

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

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

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

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

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

Allometric relationships in FRs of *C. fluminea* fed on the two phytoplankton species were not 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. reinhardtii* and  $a = 203.07 \pm 32.71$  and  $b = -1.28 \pm 0.35$  for *P. subcapitata*), although the size of the individual algal cells varied by 150% in volume (*C. reinhardtii* is larger). Thus, although the average FRs did not change with the two algal species used, at a concentration of 100,000 cells

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

This study highlights the importance of taking into account the effects of size on FR in C. 241 *fluminea* to better understand the impacts of this species on freshwater ecosystems, in particular 242 the flow of nutrients generated by filtration activity. C. fluminea's ability to filter faster as a 243 smaller individual may be part of the species' suite of r-selected species traits that enable it to 244 successfully invade novel habitats by allowing faster colonization and population establishment. 245 246 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 bivalve species disappear. Through the continuous filtration of water and its benthic lifestyle, Asian clams can strongly accumulate certain compounds including both organic (Colombo et al., 1995; Jacomini et al., 2006) and inorganic (Bonnail et al., 2016) contaminants. Several programs have thus been carried out to evaluate the potential use of *C. fluminea* as a bioindicator species (e.g. Sherman et al., 2009) and even its use in bioremediation (Rosa et al., 2014), requiring a better understanding of the factors influencing their FR. Our findings also help to refine the potential use of this species in biomonitoring and/or bioremediation programs for contamination.

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#### 258 **References**

- Araujo, R., Moreno, D., Ramos, M.A. 1993. The Asiatic clam *Corbicula fluminea* (Müller, 1774)
  (Bivalvia: Corbiculidae) in Europe. American Malacological Bulletin 10: 39-49.
- Bonnail, E., Sarmiento, A.M., DelValls, T.A., Nieto, J.M., Riba, I. 2016. Assessment of metal
  contamination, bioavailability, toxicity and bioaccumulation in extreme metallic
  environments (Iberian Pyrite Belt) using *Corbicula fluminea*. Science of the Total
  Environment 544: 1031-1044.
- Colombo, J.C., Bilos, C., Campanaro, M., Rodriguez Presa, M.J., Catoggio, J.A. 1995.
  Bioaccumulation of polychlorinated biphenyls and chlorinated pesticides by the Asiatic
  Clam *Corbicula fluminea*; its use as sentinel organism in the Río de la Plata estuary,
  Argentina. Environmental Science & Technology 29(4): 914-927.
- Coughlan, J. 1969. The estimation of filtering rate from clearance of suspensions. Marine
  Biology 2: 356-358.

271	Cranford, P., Ward, J.E., Shumway, S.E. 2011. Bivalve filter feeding: variability and limits of			
272	the aquaculture biofilter. In: Shumway, S.E. (ed) Shellfish aquaculture and the			
273	environment, chapter 4. Wiley, New York, pp 81–124			
274	Ferreira-Rodríguez, N., Sousa, R., Pardo, I. 2018. Negative effects of Corbicula fluminea over			
275	native freshwater mussels. Hydrobiologia: 810(1): 85-95.			
276	Guillard, R.R. 1975. Culture of phytoplankton for feeding marine invertebrates. In Chanley, M.			
277	H., Matoira, H. & L. Walter (eds) Culture of Marine Invertebrate Animals. Springer,			
278	Boston: 29-60.			
279	Higgins, S.N., Vander Zander, M.J., Joppa, L.N., Vadeboncoeur, Y. 2014. The effect of			
280	dreissenid invasions on chlorophyll and the chlorophyll: total phosphorus ratio in north-			
281	temperate lakes. Canadian Journal of Fisheries and Aquatic Sciences 68: 319-329.			
282	Hills, A.D., Pouil, S., Mathews, M.J. 2020. Clearance rates of freshwater bivalves Corbicula			
283	fluminea and Utterbackia imbecillis in the presence and absence of light. Aquatic			
284	Ecology 54: 1059-1066.			
285	Jacobs, P., Troost, K., Riegman, R., van der Meer, J. 2015. Length- and weight-dependent			
286	clearance rates of juvenile mussels (Mytilus edulis) on various planktonic prey items.			
287	Helgoland Marine Research 69: 101-112.			
288	Jacomini, A. E., Avelar, W.E.P., Martinêz, A.S., Bonato, P.S. 2006. Bioaccumulation of atrazine			
289	in freshwater bivalves Anodontites trapesialis (Lamarck, 1819) and Corbicula fluminea			
290	(Müller, 1774). Archives of Environmental Contamination and Toxicology 51(3): 387-			

291 391.

292	Jones, H.D., Richards, O.G., Southern, T.A. 1992. Gill dimensions, water pumping rate and body
293	size in the mussel Mytilus edulis L. Journal of Experimental Marine Biology and Ecology
294	155: 213-237.

- Kraemer, L.R., Galloway, M.L. 1986. Larval development of *Corbicula fluminea* (Muller)
  (Bivalvia, Corbicula Cea) An appraisal of its heterochrony. American Malacological
  Bulletin 4: 61-79.
- Lauritsen, D.D. 1986. Filter-feeding in *Corbicula fluminea* and its effect on seston removal.
  Journal of the North American Benthological Society 5(3): 165-172.
- Lei J., Payne B.S., Wang, S.Y. 1996. Filtration dynamics of the zebra mussel, *Dreissena polymorpha*, Canadian Journal of Fisheries and Aquatic Sciences 53: 29-37.
- Lim, K.-H., Shin, H.-C., Yang, J.-S. 2005. The influence of water temperature and food
   concentration on the filtration rates of the Asiatic clam, *Corbicula fluminea*. The Korean
   Journal of Malacology 21: 19-24.
- Marescaux, J., Falisse, E., Lorquet, J., Van Doninck, K., Beisel, J. N., Descy, J. P. 2016.
  Assessing filtration rates of exotic bivalves: dependence on algae concentration and
  seasonal factors. Hydrobiologia 777(1): 67-78.

McMahon, R.F. 1982. The occurrence and spread of the introduced Asiatic fresh-water clam,
 *Corbicula fluminea* (Müller), in North America: 1924-1982. Nautilus 96: 134-141.

McMahon, R. F. (2002). Evolutionary and physiological adaptations of aquatic invasive animals:
 r selection versus resistance. Canadian Journal of Fisheries and Aquatic Sciences, 59(7),

312 1235-1244.

- Meyhofer E. 1985. Comparative pumping rates in suspension-feeding bivalves, Marine Biology
  85: 137-142.
- Mistry, R., Ackerman, J.D. 2018. Flow, flux, and feeding in freshwater mussels. Water
  Resources Research 54: 7619-7630.
- Modesto, V., Castro, P., Lopes-Lima, M., Antunes, C., Ilarri, M., Sousa, R. 2019. Potential
  impacts of the invasive species *Corbicula fluminea* on the survival of glochidia. Science
  of the Total Environment 673: 157-164.
- Mouthon, J. 1981. Sur la présence en France et au Portugal de *Corbicula* (Bivalvia,
  Corbiculidae) originaire d'Asie. Basteria 45: 109-116.
- Møhlenberg, F., Riisgård, H.U. 1979. Filtration rate, using a new indirect technique, in thirteen
   species of suspension-feeding bivalves. Marine Biology 54: 143-147.
- Mukherjee, A., Das, S., Bhattacharya, T., De, M., Maiti, T., Kumar De, T. 2014. Optimization of
  phytoplankton preservative concentrations to reduce damage during long-term storage.
  Biopreservation and Biobanking 12: 139-147.
- Oliveira, P., Barboza, L.G.A., Branco, V., Figueiredo, N., Carvalho, C., Guilhermino, L. 2018.
  Effects of microplastics and mercury in the freshwater bivalve *Corbicula fluminea*(Müller, 1774): Filtration rate, biochemical biomarkers and mercury bioconcentration.
  Ecotoxicology and nvironmental Safety 164: 155-163.
- Oliveira, P., Lopes-Lima, M., Machado, J., Guilhermino, L. 2015. Comparative sensitivity of
   European native (*Anodonta anatina*) and exotic (*Corbicula fluminea*) bivalves to
   mercury. Estuarine, Coastal and Shelf Science 167: 191-198.

334	Ortmann, C., Grieshaber, M.K. 2003. Energy metabolism and valve closure behaviour in	the
335	Asian clam Corbicula fluminea. Journal of Experimental Biology: 206(22), 4167-4178	8.

- Payne, B. S., Miller, A. 1995. Palp to gill area ratio of bivalves: A sensitive indicator of elevated
  suspended solids. Regulated Rivers Research & Management 11: 193-200.
- Phelps, H.I. 1994. The Asiatic clam (*Corbicula fluminea*) invasion and system-level ecological
  change in the Potomac river estuary near Washington, D.C. Estuaries 17(3): 614-621.
- Pestana, D., Ostrensky, A., Boeger, W.A.P., Pie, M.R. 2009. The effect of temperature and body
  size on filtration rates of *Limnoperna fortunei* (Bivalvia, Mytilidae) under laboratory
  conditions. Brazilian Archives of Biology and Technology: 52(1), 135-144.
- Pigneur, L.M., Falisse, E., Roland, K., Everbecq, E., Deliège, J.F., Smitz, J.S., Doninck, K.V.,
  Descy, J.P. 2014. Impact of invasive Asian clams, *Corbicula* spp., on a large river
  ecosystem. Freshwater Biology: 59(3), 573-583.
- Pouil, S., Hills, A., Mathews, T.J. 2021. The effects of food quantity, light, and temperature on
  clearance rates in freshwater bivalves (Cyrenidae and Unionidae). Hydrobiologia.
  https://doi.org/10.1007/s10750-020-04472-y.
- R Development Core Team. 2020. R: A Language and Environment for Statistical Computing. R
  Foundation for Statistical Computing, Vienna.
- Riisgård, H.U. 2001. On measurement of filtration rates in bivalves the stony road to reliable
  data: Review and interpretation. Marine Ecology Progress Series 211: 275-291.

353	Riisgård, H.U., Jørgensen, B.H., Lundgreen, K., Storti, F., Walther, J.H., Meyer, K.E., Larsen,
354	P.S. 2011. The exhalant jet of mussels Mytilus edulis. Marine Ecology Progress Series
355	437: 147-164.

- Riisgård, H.U., Larsen, P.S. Pleissner, D. 2014. Allometric equations for maximum filtration rate
  in blue mussels *Mytilus edulis* and importance of condition index. Helgoland Marine
  Research 68: 193-198.
- Rosa, I.C., Costa, R., Gonçalves, F., Pereira, J.L., 2014. Bioremediation of metal-rich effluents:
  could the invasive bivalve *Corbicula fluminea* work as a biofilter? Journal of
  Environmental Quality 43(5): 1536-1545.
- Sherman, T.J., Siipola, M.D., Abney, R.A., Ebner, D.B., Clarke, J., Ray, G., Steevens, J.A. 2009.
   *Corbicula fluminea* as a Bioaccumulation Indicator Species: A Case Study at the
   Columbia and Willamette Rivers. US Army Engineer Research and Development Center,
   Washington, DC.
- Silverman H., Nichols S.J., Cherry J.S., Achberger E., Lynn J.W., Dietz T.H. 1997. Clearance of
   laboratory-cultured bacteria by freshwater bivalves: differences between lentic and lotic
   unionids. Canadian Journal of Zoology 75: 1857-1866.
- Sousa, R., Novais, A., Costa, R., Strayer, D.L. 2013. Invasive bivalves in fresh waters: impacts
   from individuals to ecosystems and possible control strategies. Hydrobiologia 735: 233 251.
- Strohmeier, T., Strand, Ø., Alunno-Bruscia, M., Duinker, A., Cranford, P.J. 2012. Variability in
  particle retention efficiency by the mussel *Mytilus edulis*. Journal of Experimental Marine
  Biology and Ecology: 412, 96-102.

375	Sylvester, F., Dorado, J., Boltovskoy, D., Juarez, A. Cataldo, D. 2005. Filtration rates of the
376	invasive pest bivalve Limnoperna fortunei as a function of size and temperature.
377	Hydrobiologia: 534, 71–80.
378	Tuttle-Raycraft S, Ackerman JD (2018) Does size matter? Particle size vs. quality in bivalve suspension
379	feeding. Freshw Biol 63:1560-1568. https://doi.org/10.1111/fwb.13184
380	Viergutz, C., Linn, C., Weitere, M. 2012. Intra- and interannual variability surpasses direct
381	temperature effects on the clearance rates of the invasive clam Corbicula fluminea.
382	Marine Biology 159: 2379-2387.
383	Way, C.M., Hornbach, D.J., Miller-Way, C.A., Payne, B.S., Miller, A.C. 1990. Dynamics of
384	filter feeding in Corbicula fluminea (Bivalvia: Corbiculidae). Canadian Journal of
385	Zoology 68: 115-120.
386	Zarauz, L., Irigoien, X. 2008. Effects of Lugol's fixation on the size structure of natural nano-

microplankton samples, analyzed by means of an automatic counting method. Journal of
Plankton Research 30: 1297-1303.

#### **Figure captions**

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

396

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

401

**Figure 3.** Relationship between whole-body fresh (g) of *C. fluminea* and the gill surface area per unit of weight (mm<sup>2</sup> g<sup>-1</sup>) estimated from Payne and Miller (1995) equation.







Figure 2



406 Figure 3

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

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

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