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Alternative food sources of native and non-native bivalves in a subtropical eutrophic lake

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Abstract:	<p>The aim of this study was to evaluate the consumption of alternative food sources (water column and sediment) and the potential competition under different conditions between Diplodon parallelipedon (native) and Corbicula fluminea (non-native). We evaluated filtration and ingestion rates of water column at 6 and 24 hours, held with and without organic matter and different phytoplankton types: needle-shaped green algae (<i>Ankistrodesmus</i> sp.) and filamentous cyanobacteria (<i>Planktothrix agardhii</i>) dominated communities. Our results confirmed higher filtration and ingestion rates per biomass unit for <i>C. fluminea</i> in presence of sediment without organic matter. However, when we compared the filtration of bivalves held in sediment with organic matter, <i>D. parallelipedon</i> rates were not significantly different from <i>C. fluminea</i> values. Moreover, in the presence of filamentous cyanobacteria, only <i>C. fluminea</i> filtration and ingestion rates decreased significantly. Our experimental results and previous field evidence concur that <i>C. fluminea</i> were not able to outcompete the native bivalves in organic matter rich sediment and cyanobacteria blooms conditions. The differential responses to the eutrophication process between exotic and native bivalves, apparently favoring the later, might buffer the potential competition interactions allowing their coexistence.</p>
Response to Reviewers:	<p>Dear Manuel,</p> <p>Firstly, we would like to thank you for really contributing comments to our work. We tried to incorporate all the suggestions received.</p> <p>Best Regards,</p>

	Soledad
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30 **Introduction**

31 Shallow lakes are among the more impacted ecosystems by human activities around the world. The main
32 perturbation is the over fertilization with nutrients (eutrophication), principally nitrogen and phosphorus
33 (Ryding & Rast, 1992; Moss, 2008; Jeppesen et al., 2010). The increase of nutrients level promotes the
34 primary production. However, in shallow lakes, two alternative states can exist within a wide range of
35 nutrient concentrations. One state dominated by aquatic plants and another dominated by phytoplankton
36 or turbid conditions. This theory, known as the Alternative State Hypothesis (ASH, Scheffer et al., 1993),
37 proposes the existence of the alternative ecosystem structures and functioning within the same
38 environmental conditions (e.g. nutrient concentration) due to several positive and negative feedbacks.
39 These feedbacks can be physical (e.g. alteration of sedimentation and resuspension rates), chemical (e.g.
40 changes in iron valence related to oxygen availability and its consequences on phosphorus retention or
41 liberation from the sediment) or even biological (e.g. changes in primary production/grazing ratios
42 mediated by direct and indirect trophic interactions, see Scheffer & Carpenter (2003) and Scheffer &
43 Jeppesen (2007)). Under eutrophic conditions cyanobacteria can dominate (Moss et al., 2011; Kosten et
44 al., 2012) the phytoplankton community interfering or limiting several critical ecosystem services, for
45 example, the drinking water supply. From the ecosystems perspective, several cyanobacteria species
46 represent a poor quality food for herbivorous (Wilson et al., 2006; Wilson & Hey, 2007) or even can be
47 toxic (Leflaive & Ten-Hage, 2007). Moreover, some species are able to control their position in the water
48 column avoiding the predation by benthic herbivores (Klemer, 1991).

49
50 A wide variety of strategies have been proposed to control the phytoplankton development in eutrophic
51 systems, the biomanipulation consists in the modification of the food web for increasing the grazing
52 pressure of herbivores, mainly through the zooplankton consumption (Shapiro et al., 1975). The primary
53 production consumption by zooplankton has been analyzed in detail in shallow lakes from temperate and
54 warm regions (e.g. Jeppesen et al., 2005; Iglesias et al., 2011; Moss et al., 2011). Contrary, the role of
55 benthic herbivores, like bivalves, is substantially less known, particularly about the coexistence of native
56 and non-native species in warm regions. Bivalves are filter-feeding organisms that consume a wide
57 particle size range. They are usually classified as omnivorous that might consume detritus, bacteria,
58 phytoplankton and zooplankton from the water column (Kreeger & Newell, 1996; Le Gall et al., 1997;
59 Davenport et al., 2000; Dupuy et al., 2000; Lehane & Davenport, 2002; Wong et al., 2003; Maar et al.,

60 2008; Davenport et al., 2011; Peharda et al., 2012). Furthermore, freshwater mussels can consume
61 organic matter present in the sediments by pedal-feeding behavior; this is a universal and primitive
62 capacity of bivalve juveniles that is also exhibited by adult organisms of several species (Reid et al.,
63 1992; Yeager et al., 1994; Hakenkamp & Palmer, 1999).

64 Bivalves, by active filter-feeding, can process large volumes of water per day removing the suspended
65 particles (Officer et al., 1982; Dame, 1996; Strayer et al., 1999; Newell, 2004; Elliott et al., 2008).
66 Therefore, bivalves can potentially play a key role in the structure and function of the entire ecosystem.
67 Indeed, the bivalves may control the abundance and composition of phytoplankton and zooplankton
68 community by direct and indirect mechanisms. This capacity depends on the amount of cleared water and
69 the size of the particles consumed (Wilson, 2003). Filtration rates have been shown to vary significantly
70 among bivalves: *Corbicula fluminea* 347-490 mL ind⁻¹h⁻¹ (Buttner & Heindinger, 1981; Silverman et al.,
71 1997); *Dreissena polymorpha* 200-300 mL ind⁻¹ h⁻¹ (Berg et al., 1996; Diggins, 2001) and *Limnoperna*
72 *fortunei* 133-350 mL ind⁻¹ h⁻¹ (Rückert et al., 2004; Sylvester et al., 2005).

73 Some of the widely distributed bivalves are invasive species, principally coming from Asia to Europe and
74 America. How these non-native species impact these ecosystems, particularly how they affect the native
75 bivalves communities, awoke the interest of many researchers (McMahon, 2002; Higgins et al., 2008;
76 Strayer et al., 2008; Cataldo et al., 2012). The scientific evidence suggested that the introduction of exotic
77 species like *Dreissena polymorpha*, *C. fluminea* or *Limnoperna fortunei* are one of the principal threats to
78 the maintenance of biodiversity at a planetary level (Darrigran, 2002). In this sense, after the introduction
79 of *D. polymorpha* into foreign aquatic systems, native freshwater bivalves species drastically declined
80 (i.e. freshwater unionoidean bivalves) (Gillis & Mackie, 1994; Schloesser & Nalepa, 1994; Ricciardi et
81 al., 1996; Strayer & Smith, 1996; Schloesser & Masteller, 1999). On the other hand, system invasions by
82 exotic bivalves, like *C. fluminea* or *D. polymorpha*, have been reported to foster an increase in the water
83 transparency and phytoplankton biomass reduction (Vanderploeg et al., 2002; Mayer et al., 2002; Zhu,
84 2006; Carroll et al., 2008; Wall et al., 2008; Strayer, 2009).

85

86 Asian clam *C. fluminea* (range size: 1-4 cm) is a good example of a successful invasive species spread
87 over the five continents. It is an r-strategist with a high level of energy efficiency; high growth rate and
88 early maturity (McMahon, 2002). This species can feed both from the water column and from the

89 sediments (Vaughn & Hakenkamp, 2001). On the other hand, South American native bivalves like
90 *Diplodon parallelopipedon* (range size: 2-10 cm), are k-strategist with slow growth and long generation
91 time. *Diplodon parallelopipedon* has only one reproductive event (spring-summer) with the additional
92 requirement of a fish-host for its parasitic larvae (Parada et al., 1989). Contrary, *C. fluminea* have at least
93 two reproductive events per year and releases a planktonic juvenile that can settle rapidly (McMahon,
94 2002).

95

96 The aim of the present study was to evaluate the filtration and ingestion rates of bivalves *D.*
97 *parallelopipedon* (native) and *C. fluminea* (non-native) that coexist in natural systems and reservoirs of
98 the coastal areas of Uruguay (Mazzeo et al., 2010). By offering two different types of phytoplankton: 1-
99 dominated by a needle-shaped green algae *Ankistrodesmus sp.* and 2- dominated by a filamentous
100 cyanobacteria *Planktothrix agardhii*, we tested the hypothesis that the non-native species has a higher
101 filtration and ingestion rate (in terms of biomass units dry weight -DW-) than native species,
102 independently of the phytoplankton composition. Furthermore, we estimated the capacity of both species
103 to feed from sediment organic matter by pedal-feeding mechanism. Thus, our second hypothesis states
104 that both species exhibit the pedal-feeding behavior which influences the phytoplankton consumption. We
105 then analyzed the relationship of these feeding behaviors with body size and biomass. We hypothesized
106 that, irrespective of the species, small-sized organisms present higher removal rates (in terms of biomass
107 units: mL g DW⁻¹ h⁻¹) than large-sized individuals. Finally, we discussed the possible interactions
108 between the native and non-native bivalves and the possible consequences on the eutrophication
109 processes.

110 **Materials and Methods**

111 Laguna del Sauce (34° 43'S, 55° 13'W) is the second water source for human water supply of Uruguay
112 (South America). It was a coastal lagoon until 1947 when the connection with the Río de la Plata river
113 through an emissary (del Potrero stream) was interrupted by the construction of a dam. Nowadays, it is a
114 shallow reservoir without inputs of salt or brackish water. It is composed by 3 interconnected shallow
115 systems (maximum depth 5m): del Sauce (4045 ha), de los Cisnes (205 ha) and del Potrero (411 ha).
116 According to the nutrient level and chlorophyll *a* concentration, Laguna del Sauce has been classified as
117 eutrophic and it presents periodical phytoplankton blooms of cyanobacteria, particularly during summer

118 (Mazzeo et al., 2010). In Laguna del Sauce coexists several filter feeding bivalves, the native *Diplodon*
119 *parallelopipedon* (Lea, 1834, Hyriidae), the exotic Asian clam *Corbicula fluminea* (Müller, 1774,
120 Corbiculidae), and the exotic golden mussel (recently appeared) *Limnoperna fortunei* (Dunker, 1857,
121 Mytilidae). *Diplodon parallelopipedon* is widely distributed across del Sauce lagoon, with an average
122 abundance of 7 ind m⁻². Contrary, *C. fluminea* is restricted mainly to sandy areas, with an average
123 abundance of 22 ind m⁻² (Garcia, 2006; Marroni, 2006; Mazzeo et al., 2010). The possible interactions
124 between native and non-native species are unknown for this shallow reservoir.

125 All the individuals used in the experiments described below were collected by free diving in Laguna del
126 Sauce and transported to the lab facilities where they were kept in oxygenated aquariums filled with de-
127 chlorinated drinking water and fed with algal cultures (principally composed by *Ankistrodesmus sp*). In
128 the laboratory, various morphometric parameters were measured for both species with the aim of
129 estimating the relationship between dry-weight (DW) and the length of individuals (see below).

130

131 **Laboratory experiments**

132 **1.-Filtration and ingestion rates test**

133 Filtration and ingestion rates estimations for both species of bivalves (*D. parallelopedon* native vs. *C.*
134 *fluminea* non native species) with absence and presence of organic matter in the sediment, were
135 conducted in 2 liter cubitainers with three cm of sediment thickness at controlled conditions of
136 temperature (20°C) and illumination (12/12 hr day/night cycle), during tests of 24h. Treatments (five time
137 replicated) consisted of: i) fed with different phytoplankton assemblages: dominated by needle-shaped
138 cultured green algae (*Ankistrodesmus sp.-A-*) and by filamentous cyanobacteria (*Planktothrix agardhii -*
139 *P-*) collected from an eutrophic urban lake and cultured at the lab; ii) body size of bivalves, small vs. large
140 individuals. The two different sizes used for *D. parallelopedon* were smaller than 6 cm and bigger than
141 7 cm respectively; in the case of *C. fluminea*, they were smaller than 2 cm and bigger than 2.5 cm
142 respectively. The bivalves were held in the same lab conditions already described being *Ankistrodesmus*
143 *sp.* culture the main food source. Bivalves selected for the tests were starved 24h prior to the beginning of
144 tests. In order to avoid settling of phytoplankton and to keep homogenized conditions inside the
145 cubitainers, a soft oxygenator device that kept a constant flux of the water was attached to each
146 experimental device. From each cubitainer, 5 mL aliquots were taken at different time intervals (0, 1, 2, 3,
147 4, 5, 6 and 24h), chlorophyll *a* (Chl *a*) was measured and filtration and ingestion rates were thus estimated
148 from the decline of Chl *a* concentration in the water from initial to final times. In Table 1 a detailed
149 description of the experimental design, including the controls used in each test is shown.

150 **2.-Pedal-feeding test**

151 The consumption of organic matter from the sediment by the two size classes of bivalves studied was
152 measured in a second type of experiment as loss of organic matter estimated by the Ignition Method
153 (burned at 550°C for 3 hrs). Sediments from Laguna del Sauce were collected from the bottom (within the
154 first ten cm) and brought to the lab. On average, organic matter (OM) content was *ca.* 20%. After heavily
155 mixing to ensure homogeneity, 50 mL were added to the bottom of each experimental device. To ensure
156 that no food was available in the water for the bivalves feeding, we used de-chlorinated tap water to fill
157 the cubitainers. Experimental conditions were kept constant at a temperature of 20°C and adequate levels
158 of dissolved oxygen were maintained with a soft oxygenator. During the experimental time (3 weeks),
159 temperature, dissolved oxygen and pH were monitored every 48h. Control replicates consisted of the

160 same treatments without the bivalves. Table 2, indicates a detailed description of the experimental design
161 including the controls used.

162 **Morphometric regression methods**

163 To calculate morphometric regressions, *ca.* 100 individuals of each species covering the length
164 distribution found in the system were sacrificed just before bringing them from the field and they were
165 measured using a digital caliper with 0.01 cm accuracy. Total length and width were recorded and the
166 entire fresh organisms were weighed with 0.001 g accuracy scale. The organisms were dried at 60°C for
167 72 hours, and then the valves and the dried bodies were weighed. Linear regression between total length
168 and total biomass was performed for both species. These regressions were later used to transform total
169 length of the individuals used in the experiments into biomass (DW). It allows expressing all the feeding
170 parameters in relation to individual biomass (e.g. filtration rate as mL g DW⁻¹ h⁻¹).

171 **Filtration and ingestion rates calculations**

172 An indirect method to calculate the filtration rate of bivalves was used in the filtration and ingestion rates
173 test (Table 1). Chlorophyll-*a in vivo* was estimated using a fluorometer (Aquafluor Handheld
174 Fluorometer, Turner Designs) and a calibration curve was performed between the fluorometer values and
175 the Chl *a* extracted by hot-ethanol protocol (see Nusch, 1980). The experimental strategy presents a
176 disadvantage because the food concentration decreases over time due to algae settling out of suspension
177 or consumption (Riisgård, 2001). To avoid this bias in the results, each treatment was compared with the
178 controls following Coughlan (1969) recommendations, and the formula used to calculate the filtration rate
179 was:

$$F = \frac{V}{nt} \left(\frac{\ln C_0}{\ln C_t} - \frac{\ln C'_0}{\ln C'_t} \right)$$

180 Where F is the individual filtering rate (mL ind⁻¹ hr⁻¹); V is the volume of water in the cubitainer; *n* is the
181 number of individuals used, *t* is the duration of experiment in hours, C₀ and C_t are initial concentration of
182 chl-*a* (µg l⁻¹) in the control (0) and in the treatments (t); C'₀ and C'_t are final chl-*a* (µg l⁻¹) in the control
183 (0) and in the treatments (t).

184 The ingestion of phytoplankton by bivalves is defined as the product of the filtration rate (F) by the mean
185 concentration of phytoplankton throughout the experiment (C). To estimate it, we used the formula
186 proposed by Frost (1972):

$$C = \frac{C_1 * \exp((k - g)t) - 1}{t(k - g)}$$

187 Where k represents algal growth ($k = [\ln(C_2/C_1)]/t$), g is the rate of removal due to grazers ($g = k - [\ln$
188 $(C_2^*/C_1^*)]/t$), C_1 and C_2 are concentrations of chl-a ($\mu\text{g l}^{-1}$) at the start and at the end of the experiment in
189 the control. C_1^* and C_2^* are concentrations of chl-a ($\mu\text{g l}^{-1}$) at the start and at the end of the experiment in
190 the different treatments.

191 **Organic matter consumption calculation**

192 At the end of the pedal feeding test, sediments were dried, weighed, burned at 550 °C for 3 h, and re-
193 weighed in order to determinate the percent of weight loss after combustion (= OM content). The change
194 in the percent of organic matter loss (OM%) between treatments (with bivalves) and controls (treatments
195 without bivalves) was estimated by subtracting final values of OM% (at the end of the experiment) from
196 the average initial value of OM%. It was estimated using the following formula:

$$\text{OM}\% = \frac{\text{MO}}{\text{Md}} \times 100$$

197 Where OM Organic matter, %, MO is mass of organic matter (grams) and Md mass of the dry soil
198 (grams).

199 **Data analysis**

200 To estimate morphometric relationships between width/length vs. dry-weight, we transformed the data
201 with $\log_{10}(X)$. Then, we applied a linear regression by minimum quadrate. In all the cases, we used
202 analysis of variance to determine if r^2 , coefficient of determination, b slope of relationship, and a intercept
203 of relationship, were statistically significantly.

204 We used multivariate analysis of variance (m-ANOVA) to detect significant differences among filtration
205 and ingestion rates treatments and controls, considering different factors: i) bivalve species (*D.*
206 *parallelipedon*, *C. fluminea*), ii) body size (small, large) and iii) food source provided (*Ankistrodesmus*

207 *sp.*, *Planktothrix agardhii*). To detect significant differences in the consumption of sediment organic
208 matter via pedal-feeding behavior, we used two-way ANOVA, considering the following two factors: i)
209 bivalve species (*D. parallelopedon*, *C. fluminea*) and ii) body size (small, large).

210 **Results**

211 Individuals of *Corbicula fluminea* collected in Laguna del Sauce at del Sauce lagoon ranged from 1.90 to
212 3.92 cm, whereas *Diplodon parallelopedon* ranged from 4.00 to 9.15 cm of shell length. We found a
213 potential relationship between dry weight of soft tissues and length for both species. After logarithmic
214 transformation of variables, a linear regression was performed and thus estimated a correlation of 90%
215 ($F_{(1,49)}=466$, $p<0.001$) between length and dry weight (coefficients $b=0.74$; $p<0.001$ and $a=-0.86$,
216 $p<0.001$, Fig. 1, Table 3) for *D. parallelopedon*. The linear regression between length-dry weight for *C.*
217 *fluminea* estimated a correlation of 83%, which was also statistically significant ($F_{(1,49)}= 304$, $p<0.001$), as
218 well as the coefficients $b=1.57$ ($p<0.001$) and $a=-1.48$ ($p<0.001$) (Fig 1, Table 3).

219 **1.-Filtration and ingestion rates tests**

220 ***Sediment without OM***

221 Independently of the body size and the phytoplankton source, the concentration of algal biomass
222 decreased in all treatments (Fig. 2). The range of filtration rate at 6 h for *D. parallelopedon* held in
223 sediments without OM and fed with both phytoplankton types was 192-496 mL g DW⁻¹ h⁻¹ (Table 4).
224 Small sized (5-6 cm) individuals of *D. parallelopedon* showed higher values of filtration rate compared
225 with large-sized (7-9 cm) ($F_{(1,19)}=32.2$, $p=0.0003$). Moreover, *D. parallelopedon* had higher filtration of
226 A compared with P ($F_{(1,19)}=12.2$, $p=0.002$). The range of filtration rate for *C. fluminea* at 6 h was 590-
227 2700 mL g DW⁻¹ h⁻¹ (Table 4). *C. fluminea* showed higher filtration rate within small sized individuals
228 (1.5-2 cm) (small>large, $F_{(1,19)}=36$, $p=0.0001$) and with A as algae source (A>P, $F_{(1,19)}=30.2$, $p=0.0001$).
229 *Corbicula fluminea* showed higher filtration rates at 6h compared with *D. parallelopedon* ($F_{(1,39)}=103.2$,
230 $p<0.0001$) regardless of the size classes and the phytoplankton tested.

231

232 The range of filtration rates at 24 h for *D. parallelopedon* held in sediments without OM, and fed both
233 phytoplankton types was 44-70 mL g DW⁻¹ h⁻¹, whereas, the range of filtration rates for *C. fluminea* was
234 123-232 mL g DW⁻¹ h⁻¹ (Fig 3). The estimations of filtration rates decreased at 24 h, but most of the

235 treatment patterns above mentioned were independently of the time period considered (Table 4). In this
236 sense, *C. fluminea* had higher filtration rates compared to *D. parallelopipedon* (at 24 h) in all size classes
237 and the phytoplankton composition tested ($F_{(1,39)}=42.75$, $p=0.0001$, Table 4, Fig. 3). In the case of *D.*
238 *parallelopipedon*, the significant differences between phytoplankton assemblages observed at 6 h
239 disappear at 24 h ($F_{(1,19)}=0.90$, $p=0.35$, Table 4, Fig. 3). In the same way, *C. fluminea* filtration rates did
240 not differ between small (1.5-2 cm) and large (2.5-3 cm) sized organisms at 24 h (Table 4).

241

242 Ingestion rate was also higher at 6 h for *C. fluminea* (123-232 $\mu\text{g Chl } a \text{ g DW h}^{-1}$) compared with *D.*
243 *parallelopipedon* (5.48-15.68 $\mu\text{g Chl } a \text{ g DW h}^{-1}$), regardless of the size classes and the phytoplankton
244 type analyzed ($F_{(1,39)}=42.75$, $p=0.0001$) (Table 4). The same pattern was observed at 24 h ($F_{(1,39)}=61.69$,
245 $p=0.001$).

246 ***Sediment with OM Test***

247 In this section, we report results of filtration tests for bivalves held with OM. We also report our
248 comparison of filtration rates (only at 24 h estimations) for both bivalves held in sediment with OM and
249 without OM. No differences were found on the filtration rates at 24h for *D. parallelopipedon* held in
250 sediment with OM and fed either phytoplankton (A: 44-82 $\text{mL g DW}^{-1} \text{ h}^{-1}$ and P: 37-72 $\text{mL g DW}^{-1} \text{ h}^{-1}$).
251 However, small-sized (5-6 cm) *D. parallelopipedon* individuals exhibited a higher filtration rate than
252 large-sized ones (7-9 cm) ($F_{(1,19)}=7.26$, $p=0.014$). No significant differences in filtration rates were
253 detected between *D. parallelopipedon* held in sediment with OM (37-82 $\text{mL g DW}^{-1} \text{ h}^{-1}$) and those held
254 without OM (40-70 $\text{mL g DW}^{-1} \text{ h}^{-1}$) ($F_{(1,39)}=0.044$, $p=0.83$, Fig. 3). The filtration rate of *C. fluminea* held
255 in sediment with OM (67-109 $\text{mL g DW}^{-1} \text{ h}^{-1}$) was lower than those observed in sediment without OM
256 (137-232 $\text{mL g DW}^{-1} \text{ h}^{-1}$) ($F_{(1,38)}=14.49$, $p=0.005$, Fig. 3). The differences between the filtration rates of
257 *C. fluminea* held without OM and fed different phytoplankton types, disappeared for *C. fluminea* held
258 with OM (A:69-109 $\text{mL g DW}^{-1} \text{ h}^{-1}$ and P:73-75 $\text{mL g DW}^{-1} \text{ h}^{-1}$, $F_{(1,19)}=1.32$, $p=0.26$). Finally, no
259 significant differences in filtration rate were found between *D. parallelopipedon* and *C. fluminea* held in
260 sediments with OM.

261

262 Ingestion rate of *D. parallelopipedon* held in sediment with OM were 0.73-1.14 $\mu\text{g Chl } a \text{ g DW}^{-1} \text{ h}^{-1}$ for
263 large-sized (7-9 cm) and 1.51-2.13 $\mu\text{g Chl } a \text{ g DW}^{-1} \text{ h}^{-1}$ for small-sized (5-6 cm) (Fig. 3). This differences

264 was marginally significant ($F_{(1,19)}=4.31$, $p=0.054$). Moreover, the ingestion rates for *D. parallelopipedon*
265 ($F_{(1,19)}=0.9$, $p=0.35$) were independent of the phytoplankton tested and there were not significant
266 differences between ingestion rates for *D. parallelopipedon* held in sediment with or without OM.
267 Ingestion rate of small sized individuals (1.5-2 cm) were 1.45-2.03 $\mu\text{g Chl } a \text{ g DW}^{-1} \text{ h}^{-1}$ and 1.49-3.31 μg
268 $\text{Chl } a \text{ g DW}^{-1} \text{ h}^{-1}$ for large specimens of *C. fluminea*, respectively (Fig. 3). This difference was not
269 significant ($F_{(1,19)}=0.58$, $p=0.45$). The ingestion rate for *C. fluminea* was higher for A (2.03-3.31 $\mu\text{g Chl } a$
270 $\text{g DW}^{-1} \text{ h}^{-1}$) compared with P (1.45-1.49 $\mu\text{g Chl } a \text{ g DW}^{-1} \text{ h}^{-1}$) ($F_{(1,19)}=3.94$, $p=0.06$). Ingestion rates for *C.*
271 *fluminea* held in sediments with OM were lower than those observed for *C. fluminea* held without OM in
272 the sediment. ($F_{(1,39)}=10.9$, $p=0.002$). The ingestion rate of *D. parallelopipedon* and *C. fluminea* held in
273 sediment with OM were not significantly different ($F_{(1,19)}=0.21$, $p=0.65$).

274 2. Pedal-feeding test

275 After 3 weeks of experiment, a significant decrease in sediment OM concentration was found in all the
276 treatments with bivalves compared with the controls ($F_{(3,67)}=20.4$, $p<0.05$). Large-sized individuals of *C.*
277 *fluminea* showed the highest OM consumption ($F_{(3,34)}=26.21$, $p<0.05$) (Fig. 4).

278 We estimated the OM consumed by dry weight of bivalves and per day (Table 5). In this case *C. fluminea*
279 showed greater consumption of sediment OM compared with *D. parallelopipedon* ($F_{(1,35)}=6.24$, $p=0.017$).
280 *C. fluminea* also showed a higher OM consumption by the large-size individuals ($F_{(1,14)}=22.4$, $p=0.001$).
281 *D. parallelopipedon* showed the same pattern but the differences in OM consumption between the sizes
282 tested was marginally significant ($F_{(1,35)}=3.31$, $p=0.08$).

283 **Discussion**

284 The experimental evidence confirmed different feeding responses of the native and non-native species
285 particularly in relation to the phytoplankton composition, presence or absence of organic matter in the
286 sediment and the size of the specimens analyzed.

287

288 **Filtration and ingestion rates tests**

289 Our results showed a sharp decrease in filtration and ingestion rates at 24h in comparison with the
290 estimations at 6 hrs. This pattern could be explained as a response to starvation of specimens previous to
291 the experiment and/or as a result of the decline in the concentration of available food. Filtration rates from
292 long term grazing experiments could be closer to natural conditions, if food supply is not a limiting factor,
293 because longer periods includes times where the specimens have lower activity due to minor consumption
294 or closing valves events (Cataldo et al., 2012; Gazulha et al., 2012). Independently of the possible causal
295 mechanisms behind the detected pattern, it is necessary to standardize the experimental grazing protocols
296 in order to obtain comparable values of filtration and ingestion rates. In this sense, experiments with
297 several and repeated food pulses at regular intervals could be a more realistic approach (Riisgård, 2001).

298

299 The filtration rates measured here for *C. fluminea* were in the same range of previous references (Buttner
300 & Heidinger, 1981; Way et al., 1990; Silverman et al., 1997). No previous information about filtration
301 rates of *D. parallelopedon* was available in the scientific literature and our data constituted the first
302 record. However, a similar range of filtration rates for *Diplodon chilensis* was previously reported by Soto
303 & Mena (1999). According to our hypothesis, higher filtration and ingestion rates per biomass unit were
304 evidenced by *C. fluminea* in comparison with *D. parallelopedon*, irrespectively of the phytoplankton
305 composition provided in the case of organic matter deprived substrates. Nevertheless, these differences
306 disappeared in presence of sediments with organic matter. These results partially agree with the higher
307 ratio filtration/biomass exhibited by *Corbicula* in comparison with native bivalves reported by Kraemer
308 (1979) and McMahon (1983).

309

310 Filtration and ingestion rates of bivalves might be affected by physiological traits (e.g. age, reproductive
311 cycle, circadian rhythms) (Cranford, 2001; Hawkins et al., 1999; Widdows, 2001; Riisgård et al., 2003;
312 Ostroumov, 2005). In our experimental conditions, age, expressed as size, affected the filtration and
313 ingestion rates, especially in the case of *D. parallelopedon*. The smaller organisms showed the higher
314 values according with our hypothesis. Environmental factors such as the quantity and quality of food can
315 also affect the feeding behavior and performance (Hawkins et al., 1999; Riisgård et al., 2003). The sizes
316 of the available particles for filter feeding and the opportunity of feeding from sediment organic matter by
317 pedal feeding behaviors were important factors in our experimental dataset. *Corbicula fluminea*

318 significantly decreased its filtration rates when the cyanobacteria *P. agardhii* dominated the
319 phytoplankton, while the native *D. parallelopedon* showed the same filtration rates independently of
320 phytoplankton types. The negative selection of cyanobacteria by *C. fluminea* was already reported by Liu
321 et al. (2009) and seems not constrained by the size of the cyanobacteria filament and/or the siphon
322 diameter. Perhaps, the dominance of *P. agardhii* represents a poor quality option as food (Wilson et al.,
323 2006; Wilson & Hey, 2007) and *C. fluminea* would prefer feeding on sediments. However, exotic
324 bivalves like *Dreissena polymorpha* are able to filter on cyanobacteria, e.g. *P. agardhii* and *Microcystis*
325 *aureginosa*, without reducing the filtration rate (Dionisio Pires et al., 2004, 2007). The response
326 evidenced here for *D. parallelopedon* agrees with previous findings by Dionisio Pires et al. (2007), who
327 demonstrated the ingestion of cyanobacteria by the native unionid bivalve *Anodonta anatine*. Our results
328 also coincide with Bontes et al. (2007) where, *A. anatina* has the same capacity to filter a small green
329 algae *Scenedesmus sp.* and filamentous *P. agardhii*. Beyond above-mentioned remarks, our data do not
330 allow a full understanding of the chronic effects of cyanobacteria ingestion, especially on bivalve's
331 growth and reproduction. Additional research is needed to clarify the possible consequences of chronic
332 feeding on cyanobacteria.

333

334 **Pedal-feeding test and alternative use of resources**

335 The evidence of OM consumption from the sediments by freshwater bivalves is very limited (Ried et al.,
336 1992; Yeager et al., 1994; Hakenkamp & Palmer, 1999). Our second hypothesis that both species can
337 feed from sedimentary OM using pedal-feeding behaviors was experimentally confirmed. These results
338 accords with former findings for *C. fluminea* (Vaughn & Hakenkamp, 2001) and constitutes the first
339 experimental evidence in the case of *D. parallelopedon*. However, we must partially reject the second
340 part of the hypothesis, the removal rate of phytoplankton declines as consequence of the alternative
341 consumption of OM from the sediment. Particularly, in the case of *D. parallelopedon* the filtration rate
342 was not affected by the availability of OM in the sediment. Inversely, *C. fluminea* presented significantly
343 lower filtration rates in presence of sediments with OM. Pedal-feeding behavior by otherwise suspension-
344 feeding bivalves may be triggered or be dependent on the quantity and quality of food resources in the
345 water column, allowing the bivalve to fulfill energetic requirements. Accordingly, the observed decline in

346 the filtration rate, particularly when cyanobacteria were the principal food source available, can be
347 interpreted as food compensation (particularly for *C. fluminea*).

348

349 The experimental data suggests an alternative use of water column or sediment resources when some of
350 them is not available or has a poor quality. The possibility of two alternative food sources is not trivial.
351 Filter feeding bivalves can survive when food quantity or quality is lacking in the water column by pedal
352 feeding behavior (Hakenkamp & Palmer, 1999). The ability to feed on different food sources has been
353 shown to uncouple predator-prey interactions (Winder & Schindler, 2004) and might release benthic filter
354 feeding bivalves from population collapses observed for example in large bodied zooplankters, like
355 *Daphnia*, or in phytoplankton.. In this sense, a great density of bivalves filter feeding can consume a
356 higher percentage of the primary production of the water column (higher than 80%), in comparison with
357 terrestrial herbivores or with the zooplankton, promoting clear water states in eutrophic conditions
358 (Ogilvie & Mitchell, 1995, Shurin et al., 2006).

359 *Integrative perspective*

360 *Corbicula fluminea* success as an invader in several environments, maybe due to their energy assimilation
361 capacity, high growth rate, early maturity and high fecundity and dispersal potential (McMahon 1983).
362 However, *C. fluminea* was not able to exclude the native bivalves of Laguna del Sauce, an ecosystem
363 with a complex spatial pattern of eutrophication consequences, cyanobacteria blooms widely distributed
364 and submerged plant dominance in limited areas (Mazzeo et al., 2010). In Laguna del Sauce, the
365 coexistence of native and exotic species has lasted, at least, 25 years. During this period, the invasive
366 species remained restricted to sandy areas of the reservoir, in contrast, *D. parallelopipedon* continued to
367 be widely distributed irrespective of sediment type (Garcia, 2006; Marroni, 2006).

368

369 Earlier scientific reports suggested that the impact of *C. fluminea* on native bivalves is much weaker than
370 other invasive mussel species like *D. polymorpha* (Strayer et al., 1999; Vaughn & Spooner, 2006).
371 Environmental factors of Laguna del Sauce like the spatial heterogeneity of the bottom sediment and the
372 relationship between sediment particle size and organic matter content might explain the co-occurrence of
373 two species of bivalves. Several sandy areas located close to the main tributaries show a high organic
374 content associated with important wetland organic matter contributions (Clemente, 2007; Rodríguez

375 Fernández, 2006). These sandy areas are dominated by *C. fluminea* (García, 2006) which showed a high
376 capacity for pedal-feeding in our experiments. However, these areas presented a limited spatial
377 distribution in this system (Mazzeo et al., 2010), the important spatial gradients of several key sediment
378 attributes may promote the spatial segregation of native and exotic bivalves buffering the competitive
379 interactions. Moreover, several massive collapses of *C. fluminea* populations have been reported in
380 Laguna del Sauce, but the causal mechanisms were not identified. Some important water quality attributes
381 associated to the eutrophication process, like temporal oxygen depletion, frequent and recurrent
382 dominance by cyanobacteria, can be important control factors of massive collapses (McMahon & Bogan,
383 2001; Werner & Rothhaupt, 2008; Vohmann et al., 2010). In contrast, native species like *Diplodon sp.* are
384 able to tolerate hypoxic environment (Grandón et al., 2008) and can also survive to prolonged
385 cyanobacterial blooms (Sabatini et al., 2012). According to this, the eutrophication process not
386 necessarily determines adverse conditions for the native species. The differential responses to the
387 eutrophication process between exotic and native bivalves can also buffer the competition interactions.

388

389 The overall experiment evidence reported and previous field studies analyzed suggest that the coexistence
390 of *Corbicula* and *Diplodon* may increase the consumption of the primary production. However, the recent
391 colonization of *Limnoperna fortunei* can change drastically the established coexistence dynamics because
392 this species uses both *Corbicula* and also *Diplodon* as substrate. New experimental evidence must be
393 generated in order to increase our knowledge about native and non-native interactions and its effects at
394 ecosystem level, as well as their potential use to control algal biomass, particularly in subtropical
395 eutrophic lakes.

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406

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681 **Table 1.** Filtration and ingestion rate in presence of sediment without OM (WO-OM) and with OM (W-
682 OM). We placed one individual by cubitanier and we consider two different body sizes for each bivalve
683 species large-sized and small (see the text). We used two phytoplankton types like sources of food 1-
684 culture of *Ankistrodesmus sp.* (A) and a community dominated by *P. agardhii* (P).

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Treatments	Body size	Biomass (g Dry weight)	Phytoplankton ($\mu\text{g/l}$)		Sediment	Replicates	Time (h)
			A	P			
<i>D. parallelopipedon</i>	Large-sized	0.860	30	30	W/WO-OM	5	24
	Small-sized	0.340	30	30	W/WO-OM	5	24
<i>C. fluminea</i>	Large-sized	0.179	30	30	W/WO-OM	5	24
	Small-sized	0.088	30	30	W/WO-OM	5	24
Control	-	0	30	30	W/WO-OM	3	24

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688 **Table 2.** Experiment of consumption of organic matter using pedal feeding behavior. We used sediment
 689 with organic matter and de-chlorinated tap water. We realized 6 replicates and 3 controls for each
 690 treatment. After 3 weeks, we measured the organic matter content.

Treatments	Body size	Biomass (g DW) by device	Phytoplankton ($\mu\text{g/l}$)		Replicates	Sediment	Duration time (weeks)
			A	P			
<i>D. parallelepipedon</i>	7-9 cm	0.860	0	0	6	OM	3
	5-6 cm	0.680	0	0	6	OM	3
<i>C. fluminea</i>	2.5-3.5 cm	0.258	0	0	6	OM	3
	1.5-2 cm	0.352	0	0	6	OM	3
CONTROL		0	0	0	3	OM	3

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712 **Table 3.** Parameters of lineal relationship between variables: width (cm) and dry weight (g) vs. length of
 713 valve (cm) (after logarithmic transformation of variables ($\text{Log}_{10}(X)$)). Parameters shows are: r^2 -coefficient
 714 of determination b slope of relationship and a intercept of relationship of *C. fluminea* and *D.*
 715 *parallelopedon*. All the relationships were significant ($p < 0.001$).

Relationship	r^2 -value	b	a	Specie
Width vs. length	0.98	0.98	0.05	<i>C. fluminea</i>
	0.94	1.06	-0.41	<i>D. parallelopedon</i>
Dry-weight vs. length	0.83	1.57	-1.48	<i>C. fluminea</i>
	0.90	0.74	-0.86	<i>D. parallelopedon</i>

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718 **Table 4.** Filtration (F mL g DW⁻¹ h⁻¹) and ingestion (I µg Chl *a* g DW⁻¹ h⁻¹) rates held in sediment without
 719 OM at 6 and 24h; for *D. parallelopipedon* and *C. fluminea*. Phytoplankton's (Phyto) communities used
 720 were: culture of *Ankistrodesmus sp.* (A) and community dominated by *P. agardhii* (P). Dry weight (DW)
 721 and size of individuals are indicated (Large (L)/Small (S)-sized). Standard errors are shown (SE).

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	F (mL g DW ⁻¹ h ⁻¹) (6h)	F (mL g DW ⁻¹ h ⁻¹) (24h)	I (µg Chl <i>a</i> gDW h ⁻¹) (6h)	I (µg Chl <i>a</i> gDW h ⁻¹) (24h)	Body size cm	Phyto
<i>D. parallelopipedon</i>	287 (20)	53 (7.87)	7.68 (0.34)	1.28 (0.19)	L	A
	496 (95)	70 (6.7)	15.68 (7.46)	1.97 (0.18)	S	
	192 (53)	44 (11.5)	5.48 (1.75)	1.22 (0.32)	L	P
	229 (75)	63 (7.5)	7.44 (2.14)	1.01 (0.21)	S	
<i>C. fluminea</i>	1400 (0.33)	218 (40.8)	49.2 (10.3)	6.14 (1.19)	L	A
	2700 (0.15)	232 (62.5)	94.2 (5.43)	7.33 (1.18)	S	
	590 (168)	137 (21.1)	18.7 (5.49)	4.51 (0.20)	L	P
	1200 (240)	123 (24.2)	37.7 (11.6)	4.02 (0.18)	S	

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726 **Table 5.** Consumption of organic matter by pedal feeding behavior per specie of bivalve and by gram of
727 dry weight (g DW) per day. Standard errors are shown (SE).

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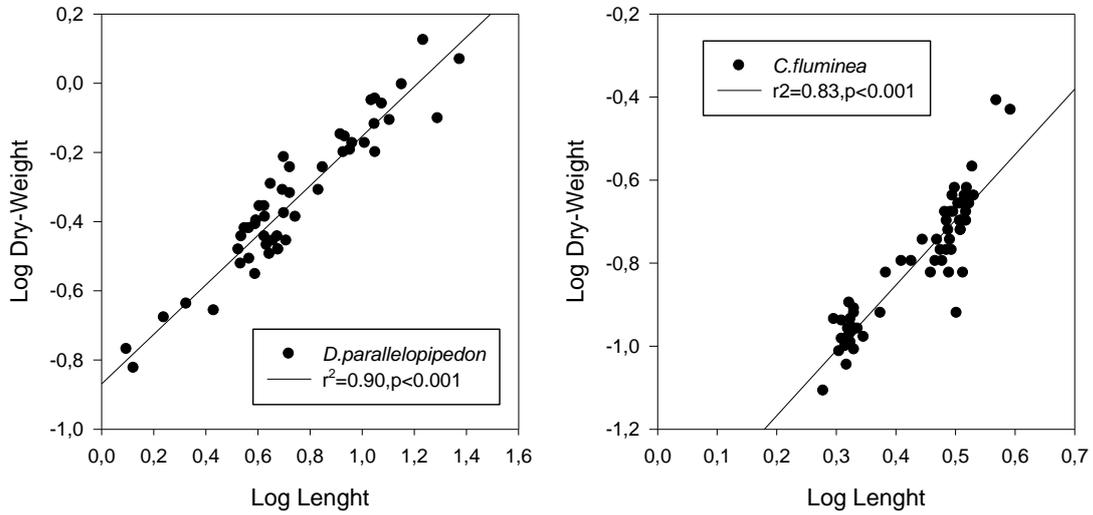
Species	mg g DW ⁻¹ day ⁻¹ (SE)	Dry weight(g) (body size range in cm)
<i>D. parallelopipedon</i>	131 (21.3)	0.86 (7-9cm)
	81 (18.2)	0.34 (5-6cm)
<i>C. fluminea</i>	257 (32)	0.179 (2.5-3.5cm)
	137 (24.3)	0.088 (1.5-2.0cm)

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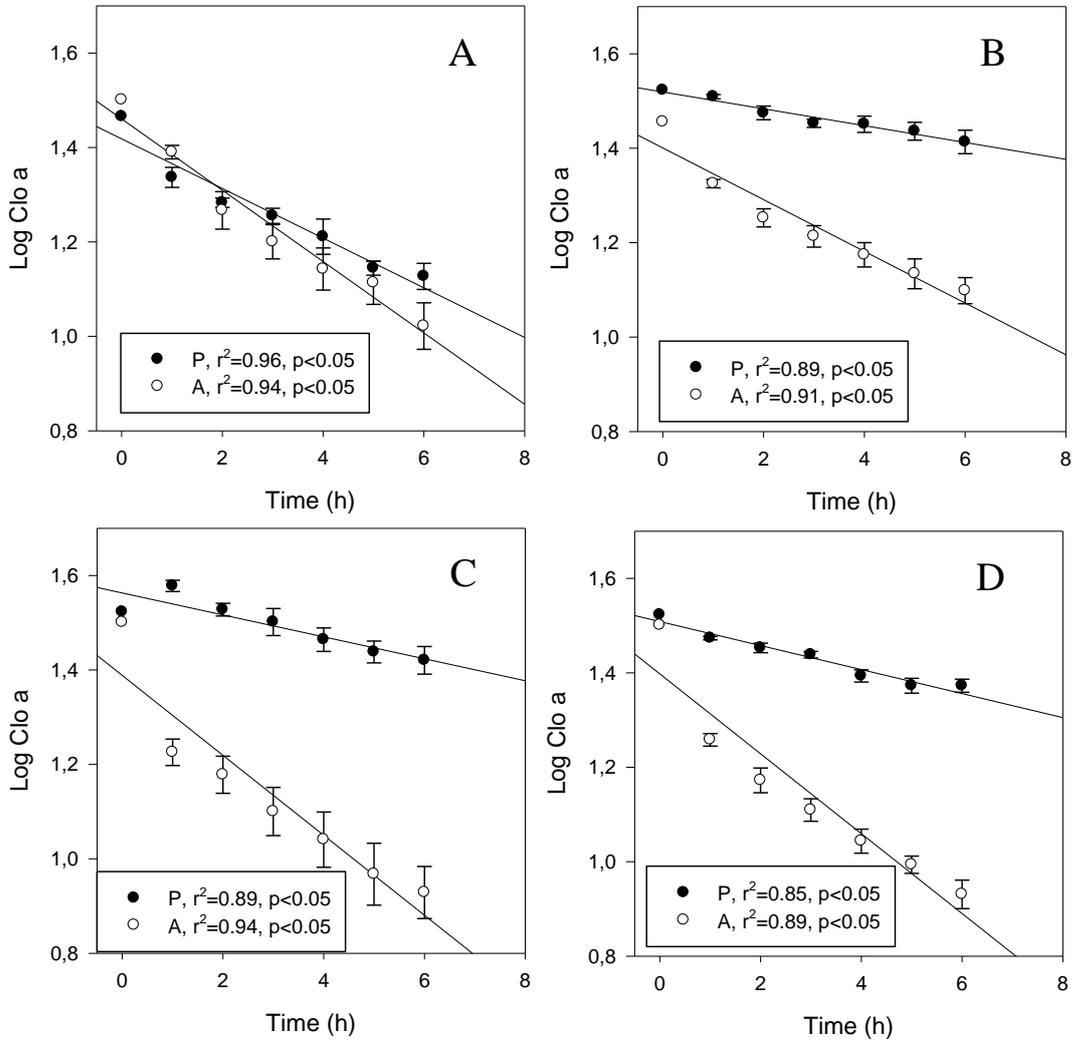
731 **FIG 1**

732 **Fig. 1.** Relationship between the Log_{10} length and Log_{10} dry weight of soft tissues for *D. parallelopedon*
733 (right) and *C. fluminea* (left). Lineal regression for *D. parallelopedon* was statistically significant as
734 well as the coefficients $b=0.74$ and $a=-0.86$ In the case of *C. fluminea* lineal regression and coefficients
735 $b=1.57$ and $a=-1.48$ were also statistically significant.



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738 **Fig. 2.** Log of chlorophyll a ($\mu\text{g l}^{-1}$) vs. time for *D. parallelopedon* (A, large-sized and B, small-sized)
 739 and *C. fluminea* (C, large-sized and D, small-sized) in test without sediment organic matter
 740 Phytoplankton: *Ankistrodesmus sp.* (white symbol) and community dominated by *P. agardhii* (black
 741 symbols). Standard error bars are shown.



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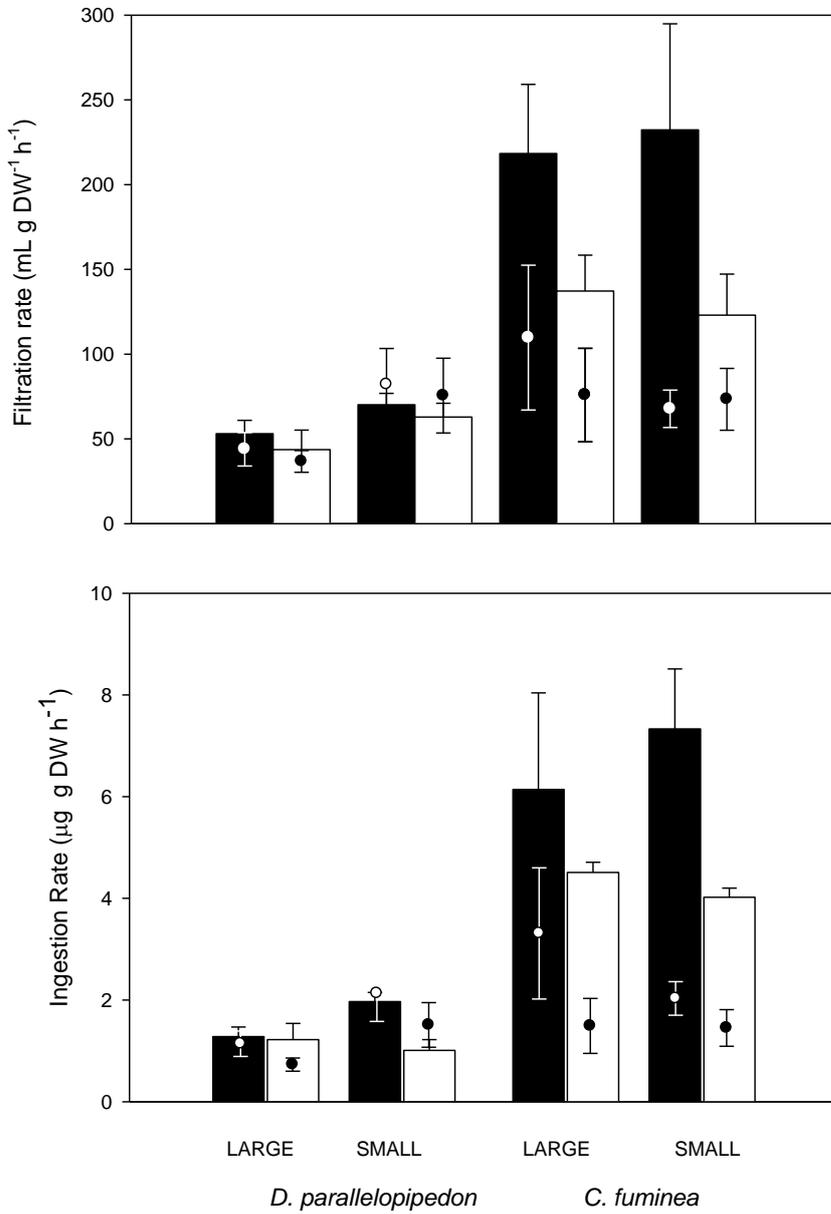
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FIG 3

Fig. 3. Comparison of filtration rates (upper panel) and ingestion rates (lower panel) at 24h between different sizes of bivalves *D. parallelipedon* and *C. fuminea* held in sediment without (bars) and with OM (circles). For different phytoplankton assemblages: *Ankistrodesmus sp.* (black bars/open circles) and *P. agardhii* (white bars/black circles).

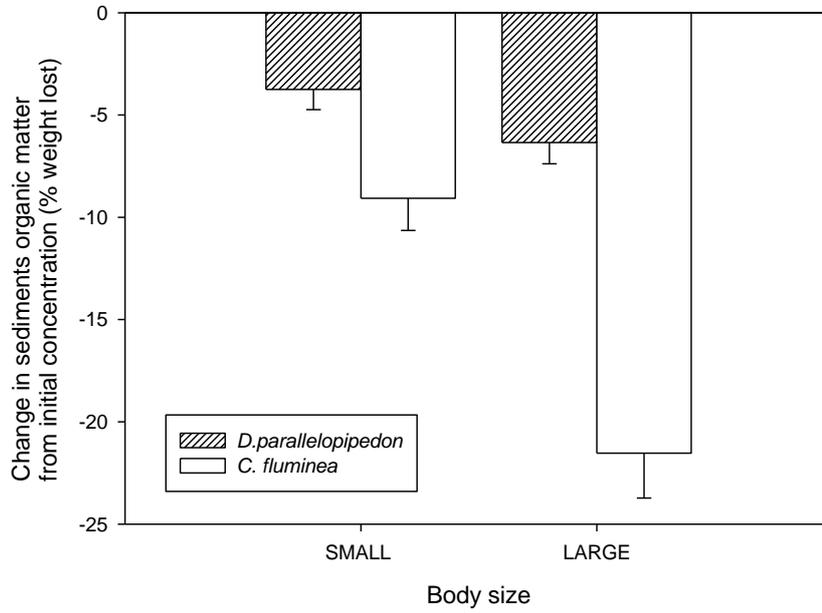


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753 **FIG. 4**

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755 **Fig. 4.** Change in sediment organic matter from initial concentration (% weight loss) by *D.*
756 *parallelopipedon* (large/small-sized) and *C. fluminea* (large/small-sized). There are not material available
757 to filter out of water column, thus this condition favored pedal-feeding. Standard error bars are shown.



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