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FRESHWATER BIVALVES

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

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Abstract 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 parallelopipedon* (native) and *Corbicula fluminea* (non-native). We evaluated filtration and ingestion rates of water column at 6 and 24 h, held with and without organic matter and different phytoplankton types: needle-shaped green algae (*Ankistrodesmus* sp.) and filamentous cyanobacteria (*Planktothrix agardhii*) dominated communities. Our results confirmed higher filtration and ingestion rates per biomass unit for *C. fluminea* in the presence of sediment without organic matter. However, when we compared the filtration of bivalves held in sediment with organic matter, *D. parallelopipedon* rates were not significantly different from *C. fluminea* values. Moreover, in the presence of filamentous cyanobacteria, only *C. fluminea* filtration and ingestion rates decreased significantly. Our experimental results and previous field evidence concur that *C. fluminea* 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.

Keywords Bivalves · Filtration and ingestion rates · Pedal feeding · *Corbicula fluminea* · *Diplodon parallelopipedon* · Eutrophication

Introduction

Shallow lakes are among the more impacted ecosystems by human activities around the world. The main perturbation is the over fertilization with nutrients (eutrophication), principally nitrogen and phosphorus (Ryding & Rast, 1992; Moss, 2008; Jeppesen et al., 2010). The increase of nutrients level promotes the primary production. However, in shallow lakes, two alternative states can exist within a wide range of nutrient concentrations. One state dominated by aquatic plants and another dominated by phytoplankton or turbid conditions. This theory, known as the alternative state hypothesis (ASH, Scheffer et al., 1993), proposes the existence of the alternative ecosystem structures and functioning within the same environmental conditions (e.g., nutrient concentration)

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due to several positive and negative feedbacks. These feedbacks can be physical (e.g., alteration of sedimentation and resuspension rates), chemical (e.g., changes in iron valence related to oxygen availability and its consequences on phosphorus retention or liberation from the sediment) or even biological [e.g., changes in primary production/grazing ratios mediated by direct and indirect trophic interactions, see Scheffer & Carpenter (2003) and Scheffer & Jeppesen (2007)]. Under eutrophic conditions, cyanobacteria can dominate (Moss et al., 2011; Kosten et al., 2012) the phytoplankton community interfering or limiting several critical ecosystem services, for example, the drinking water supply. From the ecosystems perspective, several cyanobacteria species represent a poor quality food for herbivorous (Wilson et al., 2006; Wilson & Hey, 2007) or even can be toxic (Leflaive & Ten-Hage, 2007). Moreover, some species are able to control their position in the water column avoiding the predation by benthic herbivores (Klemer, 1991).

A wide variety of strategies have been proposed to control the phytoplankton development in eutrophic systems, the biomanipulation consists in the modification of the food web for increasing the grazing pressure of herbivores, mainly through the zooplankton consumption (Shapiro et al., 1975). The primary production consumption by zooplankton has been analyzed in detail in shallow lakes from temperate and warm regions (e.g., Jeppesen et al., 2005; Iglesias et al., 2011; Moss et al., 2011). Contrary, the role of benthic herbivores, like bivalves, is substantially less known, particularly about the coexistence of native and non-native species in warm regions. Bivalves are filter-feeding organisms that consume a wide particle size range. They are usually classified as omnivorous that might consume detritus, bacteria, phytoplankton and zooplankton from the water column (Kreeger & Newell, 1996; Le Gall et al., 1997; Davenport et al., 2000, Dupuy et al., 2000; Lehane & Davenport, 2002; Wong et al., 2003; Maar et al., 2008; Peharda et al., 2011, 2012). Furthermore, freshwater mussels can consume organic matter (OM) present in the sediments by pedal-feeding behavior; this is a universal and primitive capacity of bivalve juveniles that is also exhibited by adult organisms of several species (Reid et al., 1992; Yeager et al., 1994; Hakenkamp & Palmer, 1999).

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

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

Asian clam *C. fluminea* (range size: 1–4 cm) is a good example of a successful invasive species spread over the five continents. It is an *r*-strategist with a high level of energy efficiency; high growth rate and early maturity (McMahon, 2002). This species can feed both from the water column and from the sediments (Vaughn & Hakenkamp, 2001). On the other hand, South American native bivalves, like *Diplodon parallelopipedon* (range size: 2–10 cm), are *k*-strategist with slow growth and long generation time. *D. parallelopipedon* has only one reproductive event (spring-summer) with the additional requirement of a fish-host for its parasitic larvae (Parada et al., 1989). Contrary, *C. fluminea* have at least two reproductive events per year and releases a planktonic juvenile that can settle rapidly (McMahon, 2002).

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

Materials and methods

Laguna del Sauce (34°43′S, 55°13′W) is the second water source for human water supply of Uruguay (South America). It was a coastal lagoon until 1947 when the connection with the Río de la Plata river through an emissary (del Potrero stream) was interrupted by the construction of a dam. Nowadays, it is a shallow reservoir without inputs of salt or brackish water. It is composed by three interconnected shallow systems (maximum depth 5 m): del Sauce (4045 ha), de los Cisnes (205 ha), and del Potrero (411 ha). According to the nutrient level and chlorophyll *a* concentration, Laguna del Sauce has been classified as eutrophic and it presents periodical phytoplankton blooms of cyanobacteria, particularly during summer (Mazzeo et al., 2010). In Laguna del Sauce coexists several filter-feeding bivalves, the native *D. parallelopipedon* (Lea, 1834, Hyriidae), the exotic Asian clam *C. fluminea* (Müller, 1774, Corbiculidae), and the exotic golden mussel (recently appeared) *L. fortunei* (Dunker, 1857, Mytilidae). *Diplodon parallelopipedon* is widely distributed across del Sauce lagoon, with an average abundance of 7 ind m^{-2}. Contrary, *C. fluminea* is restricted mainly to sandy areas, with an average abundance of 22 ind m^{-2} (Garcia, 2006; Marroni, 2006; Mazzeo et al., 2010). The possible interactions between native and non-native species are unknown for this shallow reservoir.

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

Laboratory experiments

Filtration and ingestion rates test

Filtration and ingestion rates estimations for both species of bivalves (*D. parallelopipedon* native vs. *C. fluminea* non-native species) with the absence and presence of OM in the sediment, were conducted in 2 l cubitainers with 3 cm of sediment thickness at controlled conditions of temperature (20°C) and illumination (12/12 h day/night cycle), during tests of 24 h. Treatments (five time replicated) consisted of: (i) fed with different phytoplankton assemblages: dominated by needle-shaped cultured green algae (*Ankistrodesmus* sp.-A-) and by filamentous cyanobacteria (*P. agardhii* -P-) collected from an eutrophic urban lake and cultured at the lab; (ii) body size of bivalves, small versus large individuals. The two different sizes used for *D. parallelopipedon* were smaller than 6 cm and bigger than 7 cm, respectively; in the case of *C. fluminea,* they were smaller than 2 cm and bigger than 2.5 cm, respectively. The bivalves were held in the same lab conditions already described being *Ankistrodesmus* sp. culture the main food source. Bivalves selected for the tests were

Table 1 Experiment of filtration and ingestion rate in the presence of sediment without OM (WO-OM) and with OM (W-OM)

Treatments	Body size (cm)	Biomass (g DW) by device	Phytoplankton (μg/l)		Sediment	Replicates	Time (h)
			A	*P*			
D. parallelopipedon	Large-sized	0.860	30	30	W/WO-OM	5	24
	Small-sized	0.340	30	30	W/WO-OM	5	24
C. fluminea	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

We placed one individual by cubitainer and we consider two different body sizes for each bivalve species large-sized and small (see the text). We used two phytoplankton types like sources of food 1—culture of *Ankistrodesmus* sp. (A) and a community dominated by *P. agardhii* (P)

Table 2 Experiment of consumption of organic matter using pedal-feeding behavior

Treatments	Body size (cm)	Biomass (g DW) by device	Phytoplankton (μg/l)		Sediment	Replicates	Duration time (weeks)
			A	*P*			
D. parallelopipedon	7–9	0.860	0	0	OM	6	3
	5–6	0.680	0	0	OM	6	3
C. fluminea	2.5–3.5	0.258	0	0	OM	6	3
	1.5–2	0.352	0	0	OM	6	3
Control		0	0	0	OM	3	3

We used sediment with organic matter and de-chlorinated tap water. We realized six replicates and three controls for each treatment. After 3 weeks, we measured the organic matter content

starved 24 h prior to the beginning of tests. In order to avoid settling of phytoplankton and to keep homogenized conditions inside the cubitainers, a soft oxygenator that kept a constant flux of the water was attached to each experimental device. From each cubitainer, 5 ml aliquots were taken at different time intervals (0, 1, 2, 3, 4, 5, 6, and 24 h), chlorophyll *a* (Chl *a*) was measured and filtration and ingestion rates were thus estimated from the decline of Chl *a* concentration in the water from initial to final times. In Table 1 a detailed description of the experimental design, including the controls used in each test is shown.

Pedal-feeding test

The consumption of OM from the sediment by the two size classes of bivalves studied was measured in a second type of experiment as loss of OM estimated by the Ignition Method (burned at 550°C for 3 h). Sediments from Laguna del Sauce were collected from the bottom (within the first 10 cm) and brought to the lab. On average, OM content was ca. 20%. After heavily mixing to insure homogeneity, 50 ml were added to the bottom of each experimental device. To insure that no food was available in the water for the bivalves feeding, we used de-chlorinated tap water to fill the cubitainers. Experimental conditions were kept constant at a temperature of 20°C and adequate levels of dissolved oxygen were maintained with a soft oxygenator. During the experimental time (3 weeks), temperature, dissolved oxygen, and pH were monitored every 48 h. Control replicates consisted of the same treatments without the bivalves. Table 2, indicates a detailed description of the experimental design including the controls used.

Morphometric regression methods

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

Filtration and ingestion rates calculations

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

$$F = \frac{V}{nt}\left(\frac{\ln Co}{\ln Ct} - \frac{\ln C'o}{\ln C't}\right)$$

where F is the individual filtering rate (ml ind^{-1} h^{-1}); V is the volume of water in the cubitainer; n is the number of individuals used, t is the duration of experiment in hours, C_0 and C_t are initial concentration of 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 (0) and in the treatments (t).

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

$$C = \frac{\mathrm{C}_1 * [\exp((k-g)t) - 1]}{t(k-g)}$$

where k represents algal growth ($k = [\ln(\mathrm{C}_2/\mathrm{C}_1)]/t$, g is the rate of removal due to grazers ($g = k - [\ln(C_2^*/C_1^*)]/t$, C_1 and C_2 are concentrations of chl-*a* (μg l^{-1}) at the start and at the end of the experiment in the control. C_1^* and C_2^* are concentrations of chl-*a* (μg l^{-1}) at the start and at the end of the experiment in the different treatments.

Organic matter consumption calculation

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

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

where: MO is mass of OM (grams) and Md mass of the dry soil (grams)

Data analysis

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

We used multivariate analysis of variance (*m*-ANOVA) to detect significant differences among filtration and ingestion rates treatments and controls, considering different factors: (i) bivalve species (*D. parallelopipedon*, *C. fluminea*), (ii) body size (small, large) and (iii) food source provided (*Ankistrodesmus* sp., *P. agardhii*). To detect significant differences in the consumption of sediment OM via pedal-feeding behavior, we used two-way ANOVA, considering the following two factors: (i) bivalve species (*D. parallelopipedon*, *C. fluminea*) and (ii) body size (small, large).

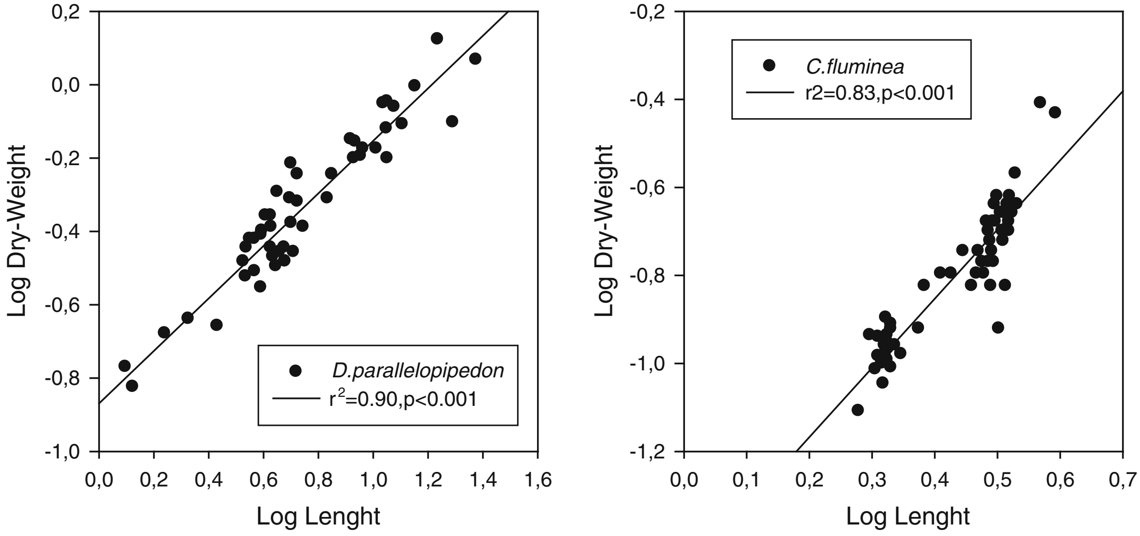

Fig. 1 Relationship between the Log_{10} length and Log_{10} dry weight of soft tissues for *D. parallelopipedon* (*right*) and *C. fluminea* (*left*). Lineal regression for *D. parallelopipedon* was statistically significant as well as the coefficients $b = 0.74$ and $a = -0.86$ In the case of *C. fluminea*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

Table 3 Parameters of lineal relationship between variables: width (cm) and dry weight (g) versus length of valve (cm) [after logarithmic transformation of variables ($\mathrm{Log}_{10}(X)$)]

Relationship	r^2 value	*b*	*a*	Species
Width versus length	0.98	0.98	0.05	*C. fluminea*
	0.94	1.06	−0.41	*D. parallelopipedon*
Dry weight versus length	0.83	1.57	−1.48	*C. fluminea*
	0.90	0.74	−0.86	*D. parallelopipedon*

Parameters shows are: r^2-coefficient of determination *b* slope of relationship and *a* intercept of relationship of *C. fluminea* and *D. parallelopipedon*. All the relationships were significant ($P < 0.001$)

Results

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

Filtration and ingestion rates tests

Sediment without OM

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

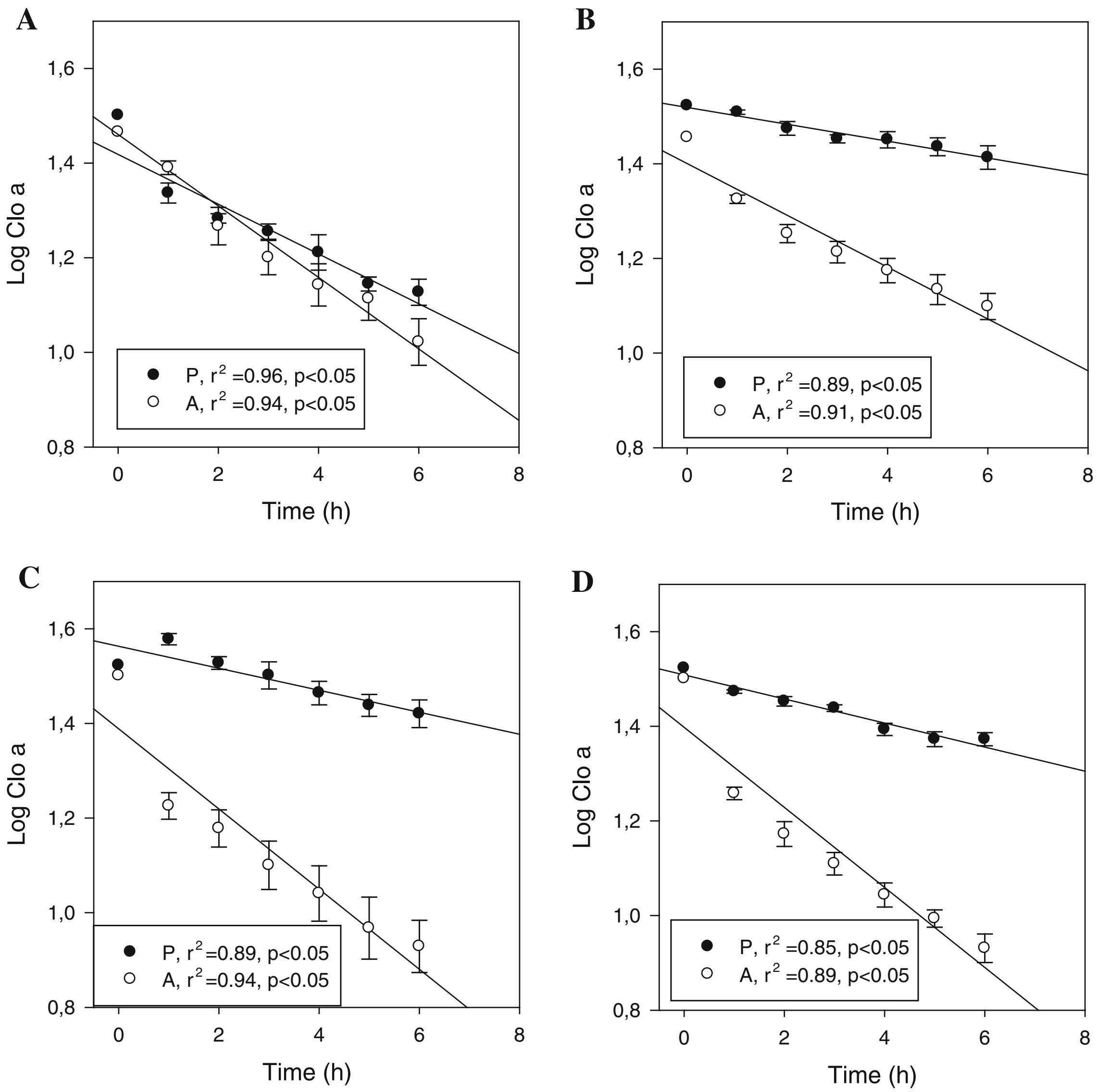

Fig. 2 Log of chlorophyll a (μg l^{-1}) versus time for *D. parallelopipedon* (**A** large-sized and **B** small-sized) and *C. fluminea* (**C** large-sized and **D** small-sized) in test without sediment organic matter Phytoplankton: *Ankistrodesmus* sp. (*white symbol*) and community dominated by *P. agardhii* (*black symbols*). Standard *error bars* are shown

The range of filtration rates at 24 h for *D. parallelopipedon* held in sediments without OM, and fed both phytoplankton types was 44–70 ml g DW^{-1} h^{-1}, whereas, the range of filtration rates for *C. fluminea* was 123–232 ml g DW^{-1} h^{-1} (Fig. 3). The estimations of filtration rates decreased at 24 h, but most of the treatment patterns above mentioned were independently of the time period considered (Table 4). In this sense, *C. fluminea* had higher filtration rates compared to *D. parallelopipedon* (at 24 h) in all size classes and the phytoplankton composition tested ($F_{(1,39)} = 42.75$, $P = 0.0001$, Table 4; Fig. 3). In the case of *D. parallelopipedon*, the significant differences between phytoplankton assemblages observed at 6 h 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 not differ between small (1.5–2 cm)- and large (2.5–3 cm)-sized organisms at 24 h (Table 4).

Ingestion rate was also higher at 6 h for *C. fluminea* (123–232 μg Chl *a* g DW h^{-1}) compared with *D.*

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 OM at 6 and 24 h; for *D. parallelopipedon* and *C. fluminea*

	F (ml g DW^{-1} h^{-1}) (6 h)	*F* (ml g DW^{-1} h^{-1}) (24 h)	*I* (µg Chl*a* g DW h^{-1}) (6 h)	I (µg Chl*a* g DW h^{-1}) (24 h)	Body size (cm)	Phyto
D. parallelopipedon	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	
C. fluminea	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	

Phytoplankton's (Phyto) communities used were: culture of *Ankistrodesmus* sp. (A) and community dominated by *P. agardhii* (P). Dry weight (DW) and size of individuals are indicated (*L* large/*S* small-sized). Standard errors are shown (SE)

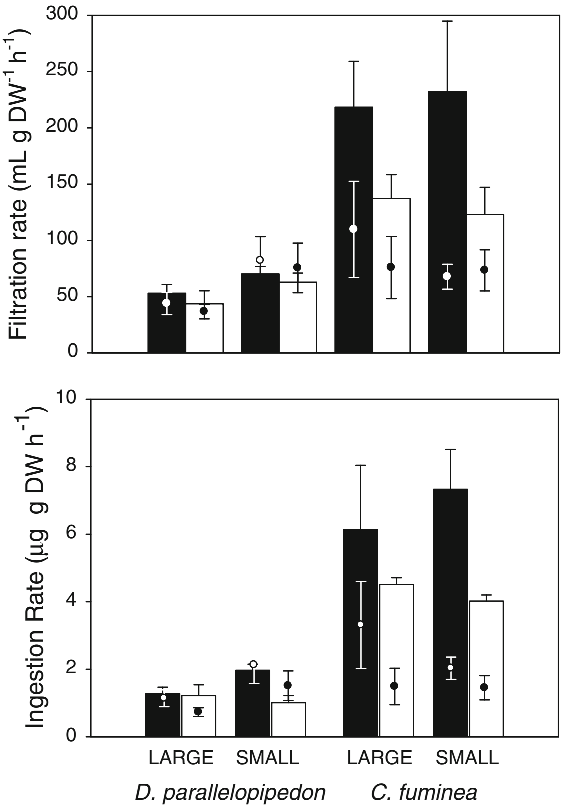

Fig. 3 Comparison of filtration rates (*upper panel*) and ingestion rates (*lower panel*) at 24 h between different sizes of bivalves *D. parallelopipedon* and *C. fluminea* held in sediment without (*bars*) and with OM (*circles*). For different phytoplankton assemblages: *Ankistrodesmus* sp. (*black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

parallelopipedon (5.48–15.68 µg Chl *a* g DW h^{-1}), regardless of the size classes and the phytoplankton type analyzed ($F_{(1,39)} = 42.75$, $P = 0.0001$) (Table 4). The same pattern was observed at 24 h ($F_{(1,39)} = 61.69$, $P = 0.001$).

Sediment with OM test

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

Ingestion rate of *D. parallelopipedon* held in sediment with OM were 0.73–1.14 µg Chl *a* g DW^{-1} h^{-1} for large-sized (7–9 cm) and 1.51–2.13 µg Chl *a* g DW^{-1} h^{-1} for small-sized (5–6 cm) (Fig. 3). These differences were marginally significant ($F_{(1,19)} = 4.31$, $P = 0.054$). Moreover, the ingestion rates for *D. parallelopipedon* ($F_{(1,19)} = 0.9$, $P = 0.35$) were independent of the phytoplankton tested and there were no significant differences between ingestion rates for *D. parallelopipedon* held in sediment with or without OM. Ingestion rate of small-sized individuals (1.5–2 cm) were 1.45–2.03 µg Chl *a* g DW^{-1} h^{-1} and 1.49–3.31 µg Chl *a* g DW^{-1} h^{-1} for large specimens of *C. fluminea,* respectively (Fig. 3). This difference was not significant ($F_{(1,19)} = 0.58$, $P = 0.45$). The ingestion rate for *C. fluminea* was higher for *A* (2.03–3.31 µg Chl *a* g DW^{-1} h^{-1}) compared with *P* (1.45–1.49 µg Chl *a* g DW^{-1} h^{-1}) ($F_{(1,19)} = 3.94$, $P = 0.06$). Ingestion rates for *C. fluminea* held in sediments with OM were lower than those observed for *C. fluminea* held without OM in the sediment. ($F_{(1,39)} = 10.9$, $P = 0.002$). The ingestion rate of *D. parallelopipedon* and *C. fluminea* held in sediment with OM were not significantly different ($F_{(1,19)} = 0.21$, $P = 0.65$).

Pedal-feeding test

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

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

Discussion

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

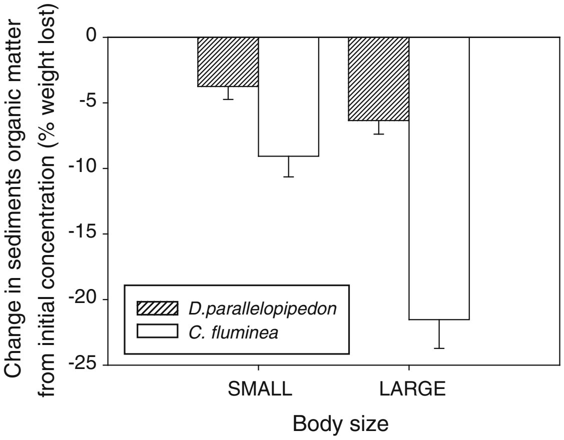

Fig. 4 Change in sediment organic matter from initial concentration (% weight loss) by *D. parallelopipedon* (large/small-sized) and *C. fluminea* (large/small-sized). There is no material available to filter out of water column, thus this condition favored pedal feeding. Standard *error bars* are shown

Table 5 Consumption of organic matter by pedal-feeding behavior per species of bivalve and by gram of dry weight (g DW) per day

Species	mg g DW^{-1} day^{-1} (SE)	Dry weight (g) (body size (cm))
D. parallelopipedon	131 (21.3)	0.86 (7–9 cm)
	81 (18.2)	0.34 (5–6 cm)
C. fluminea	257 (32)	0.179 (2.5–3.5 cm)
	137 (24.3)	0.088 (1.5–2.0 cm)

Standard errors are shown (SE)

Filtration and ingestion rates tests

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

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

Filtration and ingestion rates of bivalves might be affected by physiological traits (e.g., age, reproductive cycle, circadian rhythms) (Hawkins et al., 1999; Cranford, 2001; Widdows, 2001; Riisgård et al., 2003; Ostroumov, 2005). In our experimental conditions, age, expressed as size, affected the filtration and ingestion rates, especially in the case of *D. paralellopipedon*. The smaller organisms showed the higher values according with our hypothesis. Environmental factors such as the quantity and quality of food can also affect the feeding behavior and performance (Hawkins et al., 1999; Riisgård et al., 2003). The sizes of the available particles for filter feeding and the opportunity of feeding from sediment OM by pedal-feeding behaviors were important factors in our experimental dataset. *Corbicula fluminea* significantly decreased its filtration rates when the cyanobacteria *P. agardhii* dominated the phytoplankton, while the native *D. parallelopipedon* showed the same filtration rates independently of phytoplankton types. The negative selection of cyanobacteria by *C. fluminea* was already reported by Liu et al. (2009) and seems not constrained by the size of the cyanobacteria filament and/or the siphon diameter. Perhaps, the dominance of *P. agardhii* represents a poor quality option as food (Wilson et al., 2006; Wilson & Hey, 2007) and *C. fluminea* would prefer feeding on sediments. However, exotic bivalves like *Dreissena polymorpha* are able to filter on cyanobacteria, e.g., *P. agardhii* and *Microcystis aureginosa*, without reducing the filtration rate (Dionisio Pires et al., 2004, 2007). The response evidenced here for *D. paralellopipedon* agrees with previous findings by Dionisio Pires et al. (2007), who demonstrated the ingestion of cyanobacteria by the native unionid bivalve *Anodonta anatine*. Our results also coincide with Bontes et al. (2007) where, *A. anatina* has the same capacity to filter a small green algae *Scenedesmus sp.* and filamentous *P. agardhii*. Beyond above-mentioned remarks, our data do not allow a full understanding of the chronic effects of cyanobacteria ingestion, especially on bivalve's growth and reproduction. Additional research is needed to clarify the possible consequences of chronic feeding on cyanobacteria.

Pedal-feeding test and alternative use of resources

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

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

Integrative perspective

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

Earlier scientific reports suggested that the impact of *C. fluminea* on native bivalves is much weaker than other invasive mussel species like *D. polymorpha* (Strayer et al., 1999; Vaughn & Spooner, 2006). Environmental factors of Laguna del Sauce like the spatial heterogeneity of the bottom sediment and the relationship between sediment particle size and OM content might explain the co-occurrence of two species of bivalves. Several sandy areas located close to the main tributaries show a high organic content associated with important wetland OM contributions (Rodríguez Fernández, 2006; Clemente, 2007). These sandy areas are dominated by *C. fluminea* (Garcia, 2006) which showed a high capacity for pedal feeding in our experiments. However, these areas presented a limited spatial distribution in this system (Mazzeo et al., 2010), the important spatial gradients of several key sediment attributes may promote the spatial segregation of native and exotic bivalves buffering the competitive interactions. Moreover, several massive collapses of *C. fluminea* populations have been reported in Laguna del Sauce, but the causal mechanisms were not identified. Some important water quality attributes associated to the eutrophication process, like temporal oxygen depletion, frequent and recurrent dominance by cyanobacteria, can be important control factors of massive collapses (McMahon & Bogan, 2001; Werner & Rothhaupt, 2008; Vohmann et al., 2010). In contrast, native species like *Diplodon* sp. are able to tolerate hypoxic environment (Grandón et al., 2008) and can also survive to prolonged cyanobacterial blooms (Sabatini et al., 2011). According to this, the eutrophication process not necessarily determines adverse conditions for the native species. The differential responses to the eutrophication process between exotic and native bivalves can also buffer the competition interactions.

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

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