

***In situ* effective clearance rate measurement of mangrove oysters (*Crassostrea rhizophorae*) in a tropical estuary in Brazil**

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Abstract

Anthropogenic nutrient enrichment in estuaries induces high phytoplankton production, contributing to coastal eutrophication. Abundant natural banks of filter feeders, such as bivalves, in downstream areas may contribute to reducing symptoms of eutrophication by decreasing phytoplankton biomass and amount of material subjected to microbial regeneration.

The current concern is to what extent bivalves can control water quality and how environmental parameters can influence the filtration process and vice versa. In the present study *Crassostrea rhizophorae* (Guilding, 1818) grazing ability on suspended particles in their natural environment was determined *in situ*, using the biodeposition method and uniquely constructed sediment traps. Additionally the effect of body size on effective clearance rate (ECR) was examined using three different size groups. The experiment was conducted in the Piraquê-açu/Piraquê-mirim estuary system, (Aracruz, ES, Brazil) during the second week of June 2012 (dry season). Environmental parameters were measured together with total particulate matter (TPM, mg L⁻¹) and chlorophyll *a* analysis (CHL, µg L⁻¹) at the beginning and at the end of the experiment. Average values recorded for TPM and CHL were 5.79 mg L⁻¹ and 2.55 µg L⁻¹ respectively with very high organic seston fraction (80%). The reported effective clearance rate (ECR, in litres per hour) was 17.99 L h⁻¹g⁻¹ dry weight (DW), one of the highest reported in literature and can be associated with a high detritus content and different feeding strategies in comparison to bivalves residing in temperate environments. Weight and length (height) relationship were closely correlated ($r = 0.73$) however, clearance rate (ECR) standardized to 1 g dry tissue weight did not vary significantly among different size classes. High ECR at high particulate organic matter (POM, %) supports the belief that bivalves can exhibit ECR flexibility according to food quality.

Key words: *Crassostrea*, effective clearance rate, natural seston, oyster size, tropical ecosystem.

1. Introduction

The ecological role of bivalves and their aquaculture potential are directly related to their population clearance capacity and consequences to trophic resources (i.e. local food depletion). Moreover, bivalve feeding behaviors have direct implications for future aquaculture management including farm location optimization, predictions of carrying capacity, and the interactions with adjacent ecosystem (Cranford *et al.* 2011). The interactions between bivalve grazing and ecosystem processes has been widely studied, especially in the context of controlling eutrophication (Cloern 1982; Hily 1991). Bivalves contribute to the reduction of turbidity, thereby increasing photosynthetically active radiation (PAR) which can stimulate macro and microbenthic communities (Newell, Koch 2004) to uptake excess nutrients and limit N release back to the water column (Newell *et al.* 2002).

Clearance rate (CR) is strongly dependent on exogenous factors from which seston properties have a major influence on bivalve clearance rates and probably explains much of the variations between the clearance rate measurements that are found in the literature. In general, clearance rate initially peaks at a relatively low seston concentrations and then declines as seston concentrations increases. Increases in the organic fraction of seston usually entails decreases in feeding rates. This is probably because the animal can benefit from energy intake by preventing saturation of the gut. Moreover, studies that utilized natural seston as a food source recorded changes in CR according to short-term and seasonal variations in the concentration and composition of the seston. For example Cranford and Hill (1999) measured clearance rate *in situ* for *Mytilus edulis* (Linnaeus, 1758) and *Placopecten magellanicus* (Gmelin, 1791) at different seasons. The authors found that both species exhibit much higher clearance rate during October and November when the particle concentration and % of organic matter was the lowest in comparison to other times of the year. This study demonstrates that both species displayed high capacity for regulating clearance rate.

To date, most of the studies related to the measurement of clearance rate were performed in temperate regions under controlled conditions. Summary statistics for 68 species of oysters showed that the average value of clearance rate was 4.78 ± 0.56 ($L\ g^{-1}\ h^{-1}$ using coefficient 0.58 for standardized dry tissue weight) for seston based diets ($n = 10$) and 2.15 ± 0.49 ($n = 58$) for algae based diets (Cranford *et al.* 2011). However, most of the results are difficult to compare and interpret mainly due to inadequate use of various methodologies and differences in experimental conditions (Riisgård 2001). On the

other hand, only a few studies tried to investigate bivalve's grazing in tropical environments (Yukuhira *et al.* 1998; Hawkins *et al.* 1998b; Pouvreau *et al.* 1999, 2000; Rajesh *et al.* 2001). And of those few the majority are limited to only oligotrophic environments with seston concentrations beyond $1\ mg\ L^{-1}$ (Yukuhira *et al.* 1998; Pouvreau *et al.* 1999, 2000). Studies that investigated the clearance rate of genus *Crassostrea* at relatively similar particle concentrations as in this study reported $24.1\ L\ h^{-1}\ g^{-1}$ for *Crassostrea madrasensis* (Perston), using clearance method with algae based diet. Significantly more studies investigated the overall positive influence of using oysters to treat the effluents of shrimp farms (Jones, Preston 1999; Jones *et al.* 2001; Jones *et al.* 2002; Palmer, Rutherford 2005; Ramos *et al.* 2008; Ramos *et al.* 2009). Ramos *et al.* (2008) used mangrove oysters (*Crassostrea rhizophorae*, Guilding, 1818), for treatment of farm effluents and he reported a 62.1% reduction of turbidity, a 69.4% reduction of total suspended solids, and a 100% reduction of chlorophyll *a* after 6h of hydraulic residence time.

C. rhizophorae dominates mangrove communities in tropical and subtropical environments and presumably plays a significant role in estuarine mangrove related ecosystems worldwide. Those ecosystems are characterised by high seasonal and temporal variations in seston concentrations. Moreover, rapid urban development, deforestation of mangroves, and growing aquaculture activities are likely to increase the concentration of suspended particulates within the near future (Marques *et al.* 2004). Thus, the knowledge of how effective *C. rhizophorae* is in filtering water at specific environmental conditions can help to develop carrying capacity indicators and models that can serve as potential decisions making tool for ecosystem-based management. Given the fact that the *C. rhizophorae* is also an important fishery resource in Brazil, this knowledge will also help to define the ecological limits for sustainable aquaculture production. Moreover, the present research will try to give insight into the research debate regarding whether the grazing of bivalves is subjected to any kind of physiological regulation depending upon food quality and quantity or if it is an autonomous process that reflects only the physical properties of filter pump.

For that reason, this investigation aims to assess the grazing ability of oysters by measuring effective clearance rate (ECR), which indicates the actual volume of water cleared of particles per unit of time, under given set of environmental conditions *in situ* (Yu, Culver 1999). To distinguish from other studies that investigated the clearance rate using different methodologies, the term effective clearance rate is used in respect to this study.

2. Methodology

2.1. Study site

Piraquê-açu/Piraquê-mirim estuarine system (PAPMES) is located within the municipality of Aracruz (Espírito Santo, Brazil) 17°58'S and 40°00'W with the area of 510 ha (Fig. 1). Maximum depth at the PAPMES reaches 12 m. The tidal regime is defined as microtidal with semidiurnal mixed tides reaching a maximum amplitude of 1.4 m during the spring tide. Suspended particulate matter (SPM) varies greatly depending on the season. During the dry season, average SPM at various experimental site varies from 7.25 mg L⁻¹ (neap tide) to 17.2 mg L⁻¹ (spring tide). During the rainy season, SPM displays greater variations, ranging from 23.5 mg L⁻¹ (neap tide) to 126.3 mg L⁻¹ (spring tide) (Neves 2010). The PAPMES estuarine shoreline is covered by extensive mangrove fringes with a total combined area of 1.234 ha. The mangrove oyster normally occur in the narrow intertidal zone, found in aggregations attached to the aerial roots of red mangroves (*Rhizophorae mangle*). Distribution of the mangrove oyster is determined by the availability of substratum as limited to the narrow, vertical band found between 1.0 and 1.5 m above the 0.0 levels of spring tides. The mangrove oyster cannot survive

above the 1.5 m elevation level because of over exposure (more than 60% of each tide cycle). Correspondingly harmful, below the 1.5 elevation level, the substrate is muddy and anaerobic and inhabited by many predators (crabs, fishes, parasites) that may exert sever pressure on the oyster population (Nascimento 1991).

2.2. Collection of the oysters

To measure the actual grazing ability of oysters under natural conditions, oysters were collected from the mangrove roots during the low tide at the site where the experiment was set up. The oysters were then separated from the clusters, cleaned of parasites and measured (shell height according to Galtsoff 1964). Next, the oysters were separated by size (small 39.03±2.3; medium 54.19±1.02; large 64.56±2.3 mm) and placed in the traps. Total of 150 oysters were used. Physiological stress of *C. rhizophorae* was minimized by collecting them from the local population just before the installation of the traps.

2.3. Installation and design of the traps

New experimental methods (Yu, Culver 1999) were implemented, including the use of specially

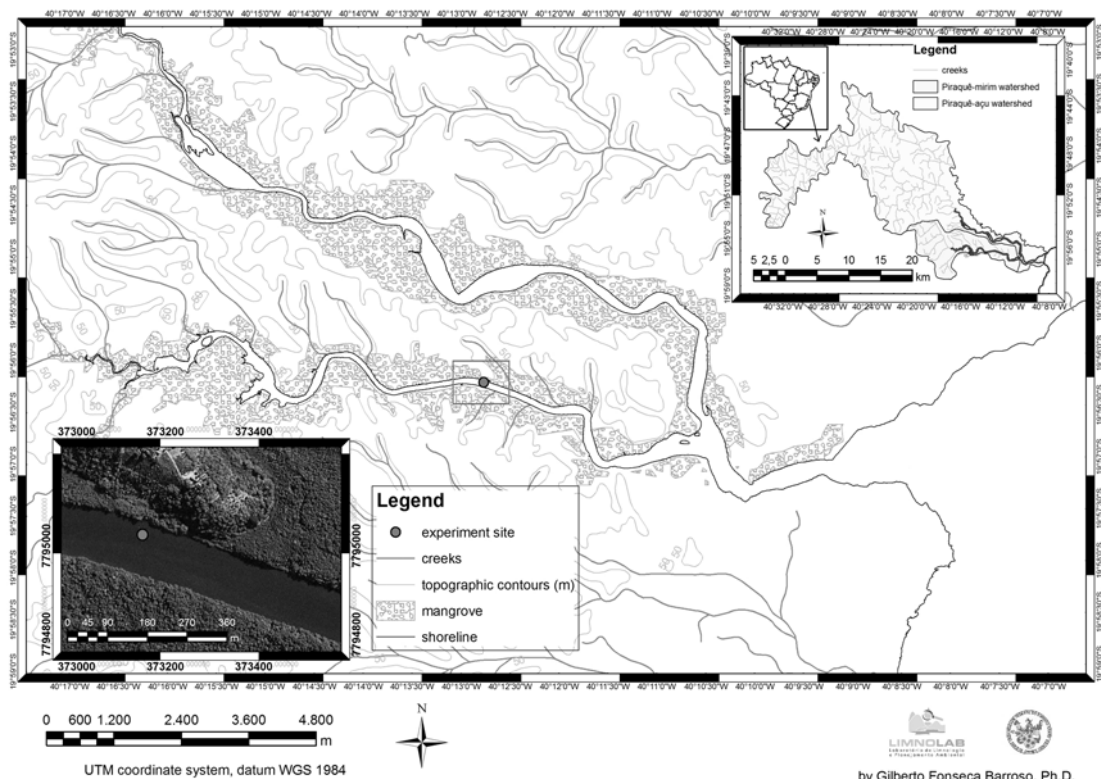


Fig. 1. Piraquê-açu/Piraquê-mirim estuarine system depicting the experimental site.

designed sediment traps that allow the collection of biodeposits quantitatively, preventing resuspension and at the same time maintaining the water flowing. To accomplish this, the traps were funnel shaped with a surface area of 300 cm² and height of 23.5 cm. The oysters were placed on the top of each trap between two layers of net forming a "pocket" to prevent escape. The top net was coarse (5 mm diameter) to maintain adequate water flow, and the supportive net had 4 mm of diameter to allow particles to pass through and settle on the bottom of the trap.

A total of 20 traps were used. They were divided into 4 groups according to oyster size: small, medium, large, and a zero-density trap to measure the background sedimentation rate incubated with empty shells in order to achieve similar surface roughness. 10 oysters per trap were used with 5 replicates of each group.

The traps were installed during the low tide (ebb tide height 0.0) approximately 20 cm below water surface and they stayed submerged for the entire duration of the experiment. The experiment was performed in June, during the dry season and it lasted one week.

2.4. Physical parameters of the water

Temperature (°C), Salinity, Dissolved oxygen (mg L⁻¹) and pH using a multiparametric probe Horiba U-51 was measured at the beginning (Survey 2), at the end (Survey 3) as well as in the week preceding (Survey 1) and succeeding (Survey 4) the experiment. Turbidity measurements collected by a portable turbidimeter (LaMotte 2020) were expressed in nephelometric turbidity units (NTU's). The speed of water flow (cm s⁻¹) was measured by the mechanical current meter (Model 2030 series). Water samples for suspended material were collected with polyethylene containers and stored in an ice-box. The water samples for chlorophyll *a* analysis were immediately filtered through the 24 mm Whatman 934 AH fiberglass filters, wrapped in aluminium foil to prevent light exposition, and stored in silica to reduce humidity.

2.5. Sample analysis

2.5.1. Seston

Seston is characterized by total particulate matter (TPM, mg L⁻¹), particulate organic matter (POM, mg L⁻¹) and particulate inorganic matter (PIM, mg L⁻¹). The organic and inorganic fractions of seston were gravimetrically determined. All the water samples collected during the experiment were filtered onto pre-ashed (450°C for 24 h) and pre-weighed 47 mm glass fiber Whatman GF/F filters and

rinsed with isotonic ammonium formate (0.5 M) to remove salts and prevent lysing of living algal cells. Total particulate matter was determined as the weight increment after drying the filters to constant weight at 110°C for 24 h, with an accuracy of 0.001 mg. Dried filters were then placed in aluminium dishes and ashed at 450°C for 24 h in a muffle furnace to determine the inorganic fraction. Particulate organic matter was determined as the difference between the total dry matter weight and the ashed weight. The ashed weights of filters that strained distilled water were used as blank controls.

The sediment traps were transported to the laboratory left for 48 h for the particles to settle down, and consequently the supernatant was siphoned off. The remaining sediment was collected, dried in the oven to constant weight and subsequently, the knowing portion of the sample was ashed in the furnace. The residual weight allowed for the calculation of the total weight of inorganic matter collected in the trap.

The analysis of chlorophyll followed the procedure of Strickland and Parsons (1972). Chlorophyll extracts were read in a TD-700 fluorometer according to the equation for chlorophyll *a* using a daylight bulb excitation (460 nm) and emission (670 nm).

2.6. Calculations of the effective clearance rate

Knowing the amount of inorganic matter (ashed weight), which has been settled by oysters over a time period, and the concentration of the particulate inorganic matter (PIM) in the water adjacent to the mussels, the volume of water cleared by the oyster was calculated as:

$$ECR = W - W_0 / CNT \text{ (L h}^{-1} \text{ ind}^{-1}\text{)}$$

where:

W – total sediment ash weight (mg) from a trap with mangrove oyster

W₀ – average ash weight from the zero-density trap (without the oysters) that represents the background sedimentation

C – PIM concentration in the ambient water (mg L⁻¹) average from samples collected at the beginning and at the end of the experiment

T – duration of incubation (h)

N – number of oysters in the trap

2.7. Statistical analysis

One-way Anova was used to compare the mean difference in between size classes for biometric variables and effective clearance rate. Multiple comparisons for means were done on significant effects using Levene Median test. Simple relationships between endogenous factors (shell lengths, tissue dry

weight) and effective clearance rate were done using Pearson correlation. All the statistical tests were done using SigmaPlot 11.0[®]. Unfortunately, during sample proceeding, two of the samples containing small size individuals had been lost therefore the number of replicates containing small size individuals was reduced from $n = 5$ to $n = 3$. Two of the replicates that were missing were calculated on the base of the average of remaining three samples.

2.7.1. Allometry

Standardization of clearance rate followed the allometric equation: $Y = aX^b$. Where Y is some measure of a part, X is a measure of the whole body or another part and 'a' and 'b' are the constants. The relationship between dry tissue weight and ECR was described by the linear equation in a logarithmic form: $\text{Log ECR} = \log a + b \log \text{DW}$. The fitted coefficient "a" and "b" were determined from a data using least square techniques.

3. Results

3.1. Environmental parameters

Total particulate matter (TPM) displayed high variability among different sampling days with the mean value for TPM from all 4 Surveys $4.83 \pm 0.88 \text{ mg L}^{-1}$ (Table I). Organic content of the TPM was around 80% in almost all of the surveys except the Survey 3 when the organic content of the seston was 61.35%. Organic content usually decreases with increasing TPM of natural seston due to diluting effect of suspended silt. Chlorophyll *a* ranged from 1.63 to $3.59 \mu\text{g L}^{-1}$ the mean

of $2.58 \pm 0.88 \mu\text{g L}^{-1}$ (Table I). Turbidity displayed wide variations ranging from 0.05 NTU during the week preceding the experiment to 12 NTU at the end of the experiment (Table I). Dissolved oxygen (mg L^{-1}), temperature ($^{\circ}\text{C}$) and pH were relatively stable throughout all measurements in comparison to other variables with an average of $4.77 \pm 0.42 \text{ mg L}^{-1}$, 7.34 ± 0.24 and $24.64 \pm 0.78^{\circ}\text{C}$ respectively (Table I). Salinity was around 24 except for Survey 3, which was 17.4 and likely is a consequence of the strong stratification corresponding to tidal activity and physical characteristics of the estuary.

3.2. Effective clearance rate

Dry tissue weight and shell height for *C. rhizophorae* for different size groups have been summarized in Table II. The length/weight morphometric relationship obtained in the present study is consistent with isometric growth and is shown to be positively correlated ($r = 0.728$) (Fig. 2).

For the 13 measurements in the present experiments, the lowest ECR value was $13.55 \text{ L h}^{-1} \text{g}^{-1}$ dry weight (DW) and the highest was $31.5 \text{ L h}^{-1} \text{g}^{-1}$ DW. Dry tissue weight ranged from 0.226 g to 0.776 g and shell height ranged from 36.5 mm to 66.5 mm (average from 10 oysters per trap).

Analyses of variance are shown in Table III. There is a significant difference in ECR between different size groups. Larger individuals filtered significantly more than the smaller individuals and more than medium size individuals ($P = 0.029$). The minimum filtration rate was 4.66 L h^{-1} for 0.22 g DW individual and the maximum was 18.8 L h^{-1} for the oysters with 0.7 g DW (Fig. 3A).

Table I. Summary of the environmental parameters measured one week before the start of the experiment (Survey 1), at the beginning of the experiment (Survey 2), at the end of the experiment (Survey 3), and one week after the experiment had finished (Survey 4). Values of TPM (Total Particulate Matter), POM (Particulate Organic Matter) and PIM (Particulate Inorganic Matter) represent mean value and range. All the parameters were measured at the same depth at which the traps were installed that is 20 cm below the 0.0 level water surface.

Environmental parameters	Survey 1 29/05/12	Survey 2 06/07/12	Survey 3 13/06/12	Survey 4 20/06/12	MEAN
Chlorophyll a ($\mu\text{g L}^{-1}$)	3.59	2.11	2.98	1.63	2.58 ± 0.88
TPM (mg L^{-1})	5.99	3.21	8.37	1.76	4.83 ± 2.55
PIM (mg L^{-1})	1.33	0.6	3.23	-	1.72 ± 1.34
POM (mg L^{-1})	4.67	2.61	5.13	-	4.14 ± 1.34
Turbidity (ntu)	0.05	2.8	12	2	4.21 ± 5.32
Dissolved oxygen (mg L^{-1})	5.33	4.85	4.4	4.49	4.77 ± 0.42
Dissolved oxygen (%)	77	70	58.2	62.7	68.4 ± 9.5
pH	7.69	7.31	7.13	7.24	7.34 ± 0.24
Temperature ($^{\circ}\text{C}$)	24.47	25.78	24.19	24.1	24.64 ± 0.78
Salinity	25.78	26.8	17.4	24.1	23.52 ± 4.22
Water flow (cm s^{-1})	-	0.0205	0.0019	0.0118	0.011 ± 0.009

Table II. Mean (\pm SD) tissue dry weight (g) and mean shell height (mm) for *C. rhizophorae* from 3 groups of different size-classes.

Group	Mean tissue dry weight (g)	Mean shell height (mm)
Small	0.27 \pm 0.046	39.03 \pm 2.3
Medium	0.56 \pm 0.088	54.19 \pm 1.02
Large	0.74 \pm 0.042	64.56 \pm 2.3

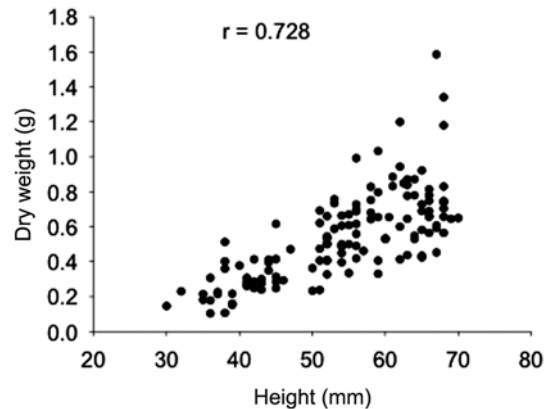


Fig. 2. Relationship between the height of the shell, and the dry tissue weight.

Opposite relationship was observed after the ECR was standardized to 1 g of DW, with smallest individuals having the highest average value for filtration rates (24.14 L h⁻¹g⁻¹ DW) and with the largest individuals exerting the lowest value of 19.48 \pm 5.36 (Fig. 3B). However, no statistically significant differences were observed among ECR standardized to 1 g of DW for the three size groups (Table III). Therefore, when considering the density of different size groups, the larger individuals are the most efficient in removing particles from the water column. When considering the entire biomass expressed in unit of mass, the differences in CR are not significant and smaller individuals may have slightly higher clearance rate than the medium and large animals.

In the allometric equation for standardization of clearance rate, the value of “a” (17.99) and “b” (0.764) were calculated according to the equation in Table IV on the basis of relationship between dry tissue weight and effective clearance rate (Fig. 4). Values “a” and “b” are fitted parameters where b represents allometric exponent (slope) and “a” is normalization constant. The “b” value is related to how fast the ECR increases relatively to body size. The “a” value is related to the ECR for the individual of 1 g dry weight. The Pearson moment correlation

Table III. Analyses of variance for biometric variables and ECR of oysters; biometric parameters were determined from the average of all individuals in each size-class trap; groups of samples with heterogeneous variances (Levene Median tests, $p < 0.05$) are marked #; asterisks denote significant differences among class-size levels, * $p < 0.01$.

Source of variation	df	Dry flesh weight		Shell height		ECR L h ⁻¹ ind ⁻¹ #		ECR for 1 g DW ind	
		MS x 10 ⁻²	F-ratio	MS	F-ratio	MS	F-ratio	MS	F-ratio
Size	2	20.4	47.89*	611.86	247.61*	57.9	8.01*	21.26	0.86
Residual	10	0.43		2.47		7.23		24.61	

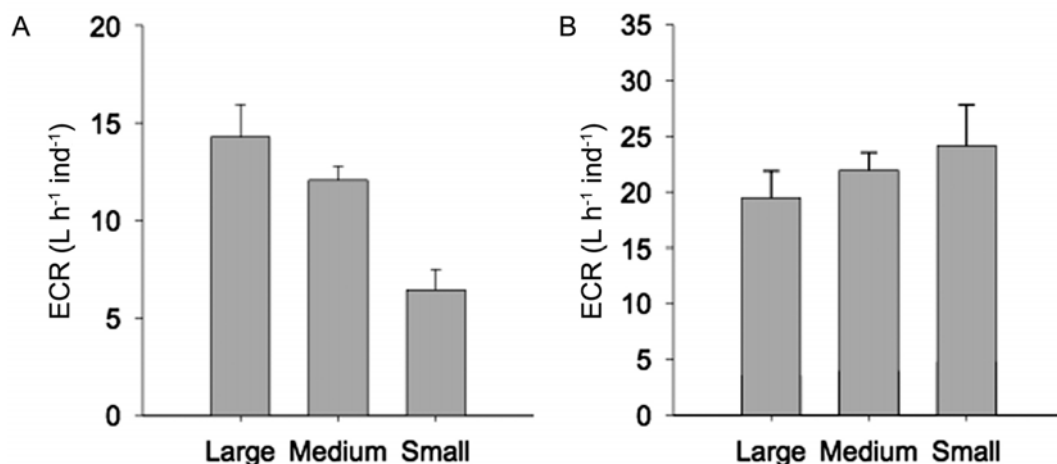


Fig. 3. Effective clearance rate for different size groups. A is the ECR not standardized; B represents ECR standardized per 1 g of DW.

showed strong positive correlation between these two factors ($r = 0.842$).

4. Discussion

The present study shows that *C. rhizophorae* residing in low to medium seston concentration during winter season have a high capacity to clear particles from surrounding water. After standardization to 1g of dry weight using coefficient $b = 0.76$, the value of effective clearance rate ($L h^{-1}$) obtained was $17.99 DW^{0.76}$, which exceeds most values found in the literature for bivalves and is one of the highest for the genus *Crassostrea* (Table V). For example, most of the studies that examined CR of *C. virginica* reported the values between $4-10 L h^{-1} g^{-1}$ (Riisgård 1988; Newell *et al.* 2005). Similar and higher values of CR were reported in more tropical and oligotrophic environments for *Pinctada margaritifera* (Linnaeus) (Table V). However, in this case, very high values of CR obtained by these authors suggest that species residing in the low seston concentrations developed special adaptation to maximize their food uptake by increasing its filtration capacity. On the other hand, Rajesh *et al.* 2001 reported $CR = 24.1 \pm 0.45 L h^{-1}$ for 100 mm *C. madrasensis*. Assuming that 100 mm *C. madrasensis* weights approximately 1 g of dry weight, this value is higher than that presently reported. The difference might come from the use of different methodologies and diets. Rajesh *et al.* 2001 used clearance method with algae based diet which results in an overall higher clearance rates than those obtained using seston based diets (Cranford *et al.* 2011). Furthermore, the oysters used in the experiment were subjected to starvation during 24 h prior to experiment what additionally could result in higher CR, especially at the beginning of the experiment.

For comparative purposes, CR is usually standardized to 1 g of dry weight, where the allometric exponent b is of great importance since it is related to the relationship between CR and the weight of the individual. Determination of exponent b is very critical as the accuracy of standardized CR value can degrade exponentially when the b -value is under or overestimated. In the present study, the b value was found to be 0.76, which is very close to the 0.73 recorded by Riisgård (1988) for *C. virgi-*

nica, and is within the range observed for bivalves (0.38-0.94) (Pouvreau *et al.* 1999). However, the b value reported in present study is the highest reported for the *Crassostrea* genus (Table V) and is in general higher than the average of 0.58 ± 0.04 reported by Cranford *et al.* (2011) for 21 different species of bivalves. Therefore, according to this b value, size specific clearance rate of *C. rhizophorae* declines faster with increasing body size than for the majority of bivalves. Lower values of b found in the majority of the literature can be a consequence of the difficulties to make accurate measurements in laboratory and the fact that usually bigger mussels are more sensitive to disturbance in the laboratory experiments relatively to smaller individuals, which did not occur in the present study (Riisgård, Møhlenberg 1979).

In relation to seston concentration the current findings are contradictory to most of the studies that reported the reduction of CR at high organic content of the seston (Hawkins *et al.* 1996; 1997; 1998a; 1998b) due to the gut saturation with organics. At high TPM concentration, when usually the fraction of organic seston is low, the clearance rate can reach even maximum rate to compensate the

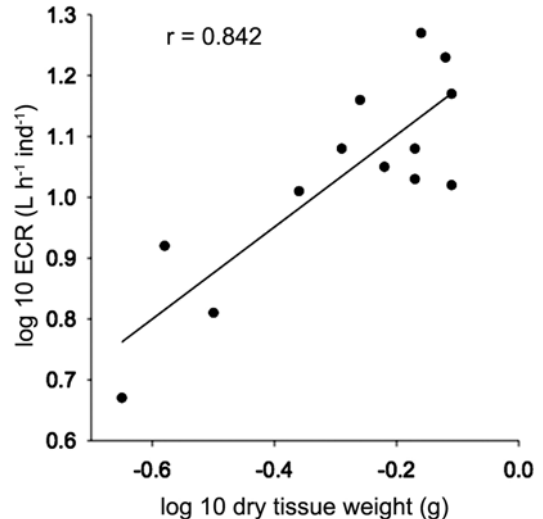


Fig. 4. The relation between the effective clearance rate and dry tissue weight converted to base 10 log.

Table IV. Allometric relationships between dry weight (g) and effective clearance rate ($g L^{-1} ind^{-1}$).

Parameters	Regression	Logarithmic equation	Allometric equation	a	b	r	n
Dry body weight (DW) and effective clearance rate (ECR)	DW on ECR	$\text{Log DW} = 0.7636x + 1.255 \text{ log ECR}$	$\text{ECR} = aDW^b$	17.99	0.764	0.842	13

Table V. Selected values of clearance rate ($L \cdot h^{-1} \cdot g^{-1}$) and filtration rate ($L \cdot h^{-1} \cdot g^{-1}$) for different species with respective coefficients b.

Reference	Species	Methods	Temperature (°C)	Clearance/Filtration rate	n	Type of diet	Weight/Size
TEMPERATE BIVALVES							
Riisgård 1988	<i>Crassostrea virginica</i>	Clearance method	27-29	F = 6.80 DW ^{0.73}	10	<i>Isochrysis galbana</i> <i>Cryptomonas</i> sp.	0.063-0.994 g DW
Bougrier et al. 1995	<i>Crassostrea gigas</i>	Flow-through system	5-32	C = 3.92 DW ^{0.50}	12-32	<i>Isochrysis galbana</i> and <i>Chaetoceros calcitrans</i>	0.1-3 g DW
Newell et al. 2005	<i>Crassostrea virginica</i>	<i>In situ</i> biodeposition	25-27	C = 7.46 to 9.62		Natural seston TPM = 13.2 mg L ⁻¹	
TROPICAL/SUBTROPICAL BIVALVES							
present study	<i>Crassostrea rhizophorae</i>	<i>In situ</i> biodeposition	25	C = 17.99 DW ^{0.76}	13	Natural seston, TPM = 5.79 mg L ⁻¹	0.27-0.74 g DW
Rajesh et al. 2001	<i>Crassostrea madrasensis</i>	Clearance method	30	C = 24.1±0.45		<i>Isochrysis galbana</i> TPM = 3-12.5 mg L ⁻¹	100-105 mm
Hawkins et al. 1998b	<i>Crassostrea belcheri</i>	Flow-through system	27	C = 4.6±1.0 DW ^{0.62}	12	Natural seston TPM = 10-23 mg L ⁻¹	0.91±0.11 g DW
Hawkins et al. 1998b	<i>Pinctada margaritifera</i>	Flow-through system	27	C = 5.5±1.3 DW ^{0.62}	6	Natural seston TPM = 10-23 mg L ⁻¹	0.86±0.24 g DW
Pouvreau et al. 2000	<i>Pinctada margaritifera</i>	<i>In situ</i> biodeposition	27-29	C = 22.0 DW ^{0.61}		Natural seston TPM = 1 mg L ⁻¹	50-180 mm
Pouvreau et al. 1999	<i>Pinctada margaritifera</i>	Flow-through system	28	C = 25.88 DW ^{0.57}	43	T-iso, TPM = 0.70 mg L ⁻¹	0.2-7.5 g DW
Yukuhira et al. 1998	<i>Pinctada margaritifera</i>	Flow-through system	25	C = 12.34 W ⁶⁰	54	T-iso, TPM = 0.5 mg L ⁻¹	0.1-10 g DW

diluting effect of suspended silt. Therefore, assuming that the bivalves are able to control their clearance rate, the expected situation would assume rather low clearance rate at such high organic content of the seston, while the opposite situation would take place if the organic seston would remain very low. Possible explanation might be related to the phytoplankton directly available for *C. rhizophorae* and high detritus content. Bivalves are able to selectively capture particles that are of higher quality value, such as phytoplankton cells silt or detritus (Newell, Shumway 1993). Moreover oysters preferentially ingest N-rich over C-rich particles (Newell, Jordan 1983). Tropical ecosystems are known to have high turnover rate of organic matter and related high detritus production. Likewise, in the PAPMES estuary, high organic content is presumably related to high detritus load that comprises the unavailable fraction of food for oysters. Weak correlation between chlorophyll *a* and organic content of TPM (not shown) additionally support the notion that larger part of POM did not originate from phytoplankton. Thus, under high POM, *C. rhizophorae* might clear the water with higher efficiency in order to offset the less preferential detritus fraction and maximize the food uptake of high quality phytoplankton. Likewise, the present study suggests that bivalves from tropical regions might have evolved different feeding strategies in relation to available quantities and qualities of seston than temperate species. This observation is in accordance with Hawkins *et al.* (1998b) who studied the feeding behaviour of a few tropical species in Malaysian mangroves in relation to seston concentration and concluded that clearances rate may be faster in tropical species versus those living in the temperate latitudes. In the future, it is important to evaluate the temporal and seasonal effect that changes of food quality and quantity in PAPMES Estuary exert on ECR of *C. rhizophorae*. Furthermore, the qualitative analysis of faeces and pseudofaeces together with phytoplankton composition and C/N ratio would enable a better understanding of the preferential uptake of mangrove oyster and their concomitant feeding strategy in relation to high POM.

Current finding integrated with river flushing rates and flow velocities data at different river discharges can give important information about the local food depletion. In the places where the high oyster densities occur and the current velocity is low, it should be expected that the oysters would filter large volumes of surrounding water, depleting local food resources. Therefore, it will have an important implication in the aquaculture activities to place the farm location at the site where the water current would ensure enough food renewal.

Oysters with a high potential for water filtration contribute to faster sediment transportation rates ultimately serving to reduce phytoplankton biomass and making systems more resilient to increases in external nutrients loads. Therefore, the use of oysters as natural biofilters in downstream areas with high organic load can be an ecohydrological measure applied in tropical ecosystems to combat algal blooms. However, grazing also entails that large amounts of nutrients are recycle back to the water column and can be available to primary producers that are not directly grazed, such as macro-algae. Therefore future studies should focus on 1) the role that oyster biodeposits have on nutrient cycling and 2) the decomposition rate at which the recycled nutrients are again available to primary producers and what part of primary production is supported by bivalves and how it affects the ecosystem.

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