

## Tolerance of Brazilian brain coral *Mussismilia braziliensis* to sediment and organic matter inputs



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### ABSTRACT

In Brazil, where reefs occur in markedly turbid environments, the relationship between sedimentation/organic matter and corals is poorly known. Thus, the *ex situ* effects of sediment with and without organic matter over the  $\Delta F/F_m$  and physical state of *Mussismilia braziliensis* were analyzed. The  $\Delta F/F_m$  and coral physical state, evaluated through the susceptibility index to sedimentation (SI), were measured in seven colonies exposed to sedimentation ( $0\text{--}450\text{ mg cm}^{-2}\text{ day}^{-1}$ ) free of organic matter after 45 days of exposure, and in 12 colonies exposed to sedimentation ( $0\text{--}500\text{ mg cm}^{-2}\text{ day}^{-1}$ ) with organic matter content (10%), in which case  $\Delta F/F_m$  was measured after 72 h and SI after 120 h. In both cases there were effects of increasing sedimentation on the SI with no effect on  $\Delta F/F_m$ . Despite the tolerance to high sedimentation rates shown by this coral, we noted that the presence of organic matter might reduce its tolerance to sedimentation stress.

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### 1. Introduction

Coral reefs are among the most diverse and productive tropical coastal ecosystems on the planet, and because they are source of goods and services to millions of people living in the tropics, they are presented as one of the most impacted environments by human interference (Bryant et al., 2000; Constanza et al., 1997; Reaka-Kudla, 1994). Degradation of these ecosystems can result in loss of biodiversity and available resources, such as fishing and tourism (Aronson et al., 2003; Bellwood et al., 2004). According to Wilkinson (2008), human activities have destroyed approximately 20% of the reefs in the world, while another 35% are threatened. Increasing the input of sediment and organic matter in marine systems has been indicated as the major cause of coral reef degradation worldwide (Carpenter et al., 2008; Hughes and Roberts, 2003a; Rogers, 1983; Szmant, 2002; Veron et al., 2009). Moreover, decreasing water quality is generally related to either drilling and dredging ocean substrate or as a consequence of pollution and misuse of land in coastal areas (Godinot et al., 2011; Wesseling et al., 1999).

Increasing the concentration of sediment in the water may affect corals in various ways. Sediment particles and associated organic matter in suspension cause reduction of luminosity, which directly affects the photosynthetic performance of zooxanthellae endosymbionts, responsible for up to 90% of the nutrition of corals (Fabricius, 2005; Hoegh-Guldberg, 1999; Muscatine, 1990). Deposition of large amounts of sediment on reefs may also cause coral smothering, abrasion, increase of energy consumption for the removal of particles, and reduction of planulae larvae recruitment (Rogers, 1990; Riegl and Branch, 1995; Wesseling et al., 1999; Yentsch et al., 2002). The increased level of organic matter causes sediment flocculation, which enhances the damages from smothering, and proliferation of disease-causing pathogens (Fabricius and Wolanski, 2000; Haapkyla et al., 2011). Furthermore, increasing the supply of organic matter can compromise the health of the reef community, usually by promoting phase shift scenarios, through the replacement of reef-building corals by algae or other non-builders and more resistant organisms (Szmant, 2002; Mumby, 2009; Norström et al., 2009). This situation may endanger reef complexity (Dunn et al., 2012; Hughes et al., 2007; Szmant, 2002). Therefore, both increased sedimentation and organic matter may adversely affect the growth and reproductive success of corals on impacted reefs (Gilmour, 1999; Riegl, 1995; Reopanichkul et al., 2009).

The declining health of corals due to a decrease in water quality of coastal areas is noticeable in several parts of the world, such as in the northern Atlantic and Pacific (Fabricius, 2005; Rogers, 1983).

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In Brazil, the negative effects of increased concentrations of sediment and organic matter in coastal reefs have also been reported (Costa Jr. et al., 2000; Dutra et al., 2006; Leão et al., 2006; Reis and Leão, 2003). Unlike other parts of the world where reefs are under oligotrophic conditions (Fabricius and Wolanski, 2000; Kleypas et al., 1999), in Brazil, reef ecosystems often occur in environments naturally exposed to high rates of sedimentation, due to a sea level regression during the Holocene, and large river flows off the coast (Leão and Kikuchi, 2005). These extreme conditions, characterize these reefs as marginal systems, a situation that is the most probable cause for the tolerance of most Brazilian coral species to high sedimentation rates (Leão et al., 2003; Segal and Castro, 2011; Suggett et al., 2012). Nevertheless, the direct effect of sediments and organic matter on the metabolism of Brazilian corals, as well as their defense mechanisms, tolerance and resilience of key species, are still unanswered questions.

Thus, the present study aimed first to investigate, under controlled laboratory experiments, the stress in colonies of *Mussismilia braziliensis* caused by sedimentation and input of organic matter. In particular we attempted to understand the effects of exposure to different concentrations of sediment associated or not with organic matter on: (1) the photosynthetic metabolism, evaluated from the photobiological efficiency, and (2) the physical susceptibility of colony tissue to sedimentation, based on a quantitative susceptibility index developed in the present study. Secondly, susceptibility indexes of colonies exposed to sediment without organic matter were compared with susceptibility indexes of colonies exposed to sediment combined with organic matter. *M. braziliensis* is an endemic species, which currently has the greatest geographical confinement of all hard corals in Brazil, restricted to the country's eastern coast (Castro and Pires, 2001). It is also the main builder of the Abrolhos reefs, the largest reef complex in the southern Atlantic Ocean (Leão et al., 2003). The results of this study therefore will be useful to clarify the effects of increased sedimentation and the input of organic matter on Brazilian corals, which are caused, among other reasons, by coastal development and deforestation. The results will also allow the comparison with other ecosystems that have been more minutely studied, such as reefs in the Caribbean and Australia (Lough et al., 2002; Nughes and Roberts, 2003a, 2003b; Sofonia and Anthony, 2008). Moreover, these results can assist in the management of these environments, considered as biodiversity 'hot spots', as a means to hinder destructive human impacts (Halpern et al., 2008).

## 2. Methods

### 2.1. Material collection and preparation

The effect of sediment associated or not with organic matter on the physical state of the tissue of *M. braziliensis* colonies and on the photosynthetic efficiency of their symbiotic algae was tested in the indoor coral aquaria of the Federal University of Bahia, between August 2011 and March 2012. Nineteen colonies of *M. braziliensis* with 8 cm in average diameter were collected at 3–5 m depth in the Pedra de Leste reef, in the Abrolhos region (PDL, 17°46.550S, 39°03.050W). Corals were kept in two 40 l aquaria, for acclimatization, with synthetic seawater (Red Sea Salt and deionized water) for 60 days to minimize the stress caused by their collection and transport. Corals remained under optimal and uniform conditions of light ( $1000 \pm 28$  lux), temperature ( $26 \pm 0.2$  °C), pump agitation ( $650 \text{ l h}^{-1}$ ), salinity (36 psu) and physicochemical water parameters such as  $\text{NO}_2$  (0–0.1 ppm),  $\text{NO}_3$  (0 ppm),  $\text{PO}_4$  (0 ppm), Ca (450 ppm),  $\text{O}_2$  (8–9 ppm), alk (3.2 m Eq/l) and pH (8.4), as used by Oliveira et al. (2008). During the acclimatization period the aquaria water was changed once a week.

Muddy sediment was collected at a depth of 5 m in the Caravelas river channel (SED, 17°45.364 S, 39°13.407W), which is undergoing dredging activities. In the lab, the sediment was washed, dried, weighted and separated in two parts: one remained as it was and the other underwent a process to remove organic matter using hydrogen peroxide ( $\text{H}_2\text{O}_2$ ). The relative amount of organic matter ( $9.31\% \pm 0.10$ ) present in the sediment was determined by weighting a sample before and after its removal with hydrogen peroxide. The sediment was classified as fine silt according to the analysis carried out using a diffraction laser granulometer (Horiba Partica LA-950), and basically consisted of siliciclastic components ( $90.69 \pm 0.10\%$ ).

### 2.2. Experimental system and data collection

After acclimatization, the corals were moved to five experimental thermostatic systems. Each system contained four glass chambers (4 l) with synthetic seawater (36 psu), which were placed within a 60 l aquarium, with fresh, warm ( $26 \pm 0.2$  °C) and circulating ( $650 \text{ l h}^{-1}$ ) water. The lighting system was similar to that described for the acclimatization system. Only one of the systems had three glass chambers in the 60 l aquaria. A colony of *M. braziliensis* was placed in each 4 l chamber randomly chosen from the acclimatization aquaria. The concentration of sediment with or without organic matter to be inserted into the chamber was also randomly set.

#### 2.2.1. Experiment 1: sediment free of organic matter

Specific concentrations of sediment without organic matter were added to seven 4 l chambers, which were kept in the thermostatic systems. The concentrations were:  $0 \text{ mg cm}^{-2} \text{ day}^{-1}$ , representing the optimal control condition,  $15 \text{ mg cm}^{-2} \text{ day}^{-1}$ , representing the sedimentation rate of the PDL reef (Dutra et al., 2006), 50, 150, 250, 350 and  $450 \text{ mg cm}^{-2} \text{ day}^{-1}$ . The water of each chamber was stirred, daily, for 2 min with a glass rod to simulate events of sediment resuspension and deposition. Colonies of *M. braziliensis* were exposed to their respective treatments for 45 days, after which one colony died. Every two days the water and the amount of sediment specific to each chamber were replaced.

**2.2.1.1. Fluorometry of chlorophyll a (Chl a).** The photosynthetic efficiency of zooxanthellae was determined by measuring the fluorescence of photosystem II (PS II) of Chl a, which was induced with a Diving-PAM pulse-amplitude modulated chlorophyll fluorometer (Walz, Germany). Chlorophyll fluorescence was measured at a distance of approximately 3 mm from the coral surface. Hennige et al. (2008) have detailed information on the operation and the configuration used for the Diving-PAM. Before the experiment, all colonies showed the characteristic color of the species, indicative of no-bleaching conditions. The dark-adapted photochemical efficiency ( $\Delta F/F_m$ ) of the seven colonies, including the control colony, was measured after 45 days of exposure to their respective concentrations of sediment free of organic matter. This measurement was performed before beginning the daily illuminated period of the aquaria. Three fluorescence measurements were carried out randomly on the top of each colony.

**2.2.1.2. Susceptibility index ( $SI_{Mb}$ ).** A quantitative susceptibility index for *M. braziliensis* ( $SI_{Mb}$ ) to sedimentation was developed to evaluate the effect of the sediment free of organic matter on the physical state of the colonies tissues. Values were assigned to each of the different types of tissue injury observed on coral surfaces at the end of the experiment, following an increasing sequence according to the severity of the physical stress in question. The percentage of affected colony area by a type of identified injury

**Table 1**

Scores attributed to each of identified physical damages (PD) and for each category that represents the percentage of colonies affected area (AA).

Physical damage (PD)		Affected area (AA)	
Description	Score	%	SCORE
No damage	0	0	0
Polyps inflation	4	1–20	2
Abrasion	6	21–40	4
Smothering	8	41–60	6
Necrosis	18	61–80	8
<sup>a</sup>	<sup>a</sup>	81–100	10

<sup>a</sup> Represent absence of other physical damage (PD).

was also considered. Four symptomatic injuries were identified (Table 1). The score attributed to necrosis represents the sum of the values set for the other three damages. The greater weight established for this type of injury is due to the impossibility of reversing this condition. The percentage of affected area for each kind of physical damage observed in the tissue was also estimated for each of the seven colonies and, again, a specific score was given for the previously defined area size class (Table 1). In each colony, up to two types of physical damages were observed, which were denominated as PD1 and PD2 respectively (Table 2).

Thus, after 45 days, the  $SI_{Mb}$  of the seven colonies of *M. braziliensis* exposed to sediment free of organic matter, including the control colony, was established. The index was calculated from the sum of the product of the types of physical damages identified in *M. braziliensis* ( $PD_{Mb}$ ) and the percentages of the colony's affected area ( $AA_{Mb}$ ) for each kind of physical damage observed, as follows:

$$SI_{Mb} = \sum (PD_{Mb} * AA_{Mb})$$

Considering as an example one of these seven colonies, after 45 days of experimentation subjected to a specific sedimentation disturbance. Supposing this colony showed 50% of its polyps inflated (polyp inflation) and another 30% of the colony area presented tissue necrosis. The SI would be calculated from the sum of the products between the scores defined for these two different types of physical damages observed (polyp inflation as PD1 and necrosis as PD2) and their respective scores attributed for the percentage of affected colonial area (50% and 30% respectively), as specified in Table 1. Therefore, in this example the SI would be equivalent to:

$$SI_{Mb} = (4*6) + (18*4); SI_{Mb} = 96$$

Before experimentation corals did not have any apparent physical damage in their tissue.

### 2.2.2. Experiment 2: sediment with organic matter

Twelve different concentrations of sediment with organic matter (0, 15, 50, 100, 150, 200, 250, 300, 350, 400, 450 and

500 mg cm<sup>-2</sup> day<sup>-1</sup>) were added to twelve 4 l glass chambers, kept in the thermostatic system. The number of concentrations was greater (in comparison with the first experiment) to have a more detailed description of the impact of the sediment on the corals. Water in each chamber was stirred daily. The maximum exposure time of corals to this treatment was five days (120 h), after which one of the colonies died.

**2.2.2.1. Fluorometry of chlorophyll a (Chl a).** Again, before the experiment all colonies showed no signs of bleaching. The dark-adapted photochemical efficiency ( $\Delta F/F_m$ ) of each colony, including the control colony, was estimated after 72 h of exposure to the respective concentrations of sediment with organic matter. An average value of efficiency was obtained from three fluorescence measurements taken randomly from the top of each colony.

**2.2.2.2. Susceptibility index ( $SI_{Mb}$ ).** After 120 h of exposure, the  $SI_{Mb}$  of the 12 colonies exposed to sediment with organic matter, including the control colony, was established. Again, before experimentation corals did not show physical damages.

The  $SI_{Mb}$  of the colonies exposed to concentrations of 15, 50, 150, 250, 350 and 450 mg cm<sup>-2</sup> day<sup>-1</sup> of sediment free of organic matter was compared with the  $SI_{Mb}$  of colonies exposed to the same amounts of sediment with organic matter ( $n=6$  colonies per treatment), after 120 h of exposure. The control colonies were not included in these analyses.

### 2.3. Data analysis

For both the seven colonies exposed to sediment without organic matter and the 12 colonies exposed to sediment with organic matter, four linear regressions were performed plotting the sedimentation rate (mg cm<sup>-2</sup> day<sup>-1</sup>) against the  $\Delta F/F_m$  of *M. braziliensis* zooxanthellae and against the calculated  $SI_{Mb}$  for the sediment without organic matter and the sediment with organic matter. The regression approach was chosen because its power is not determined by the number of replicates, but by the number of factors and experimental units (Cottingham et al., 2005). In our case, the experimental units are the number of different sediment concentrations/colonies. Thus, to minimize impact in the sampling site we decided to reduce replication and apply a single factor experimental design.

The  $SI_{Mb}$  of colonies exposed to the six concentrations (previously mentioned) sediment, with and without organic matter, were compared using the nonparametric Mann–Whitney test. A non-parametric analysis was used due to the heteroscedasticity of the dependent variable in question. For all analyses significance level ( $\alpha$ ) was equivalent to 0.05.

**Table 2**

SI calculated for each of seven colonies exposed to sediment without organic matter after 45 days of sedimentation exposure.

Colony	Sedimentation rate (mg cm <sup>-2</sup> day <sup>-1</sup> )	PD 1	AA (%)	PD 2	AA (%)	SI $\Sigma(PD*AA)$
<i>Colonies exposed to sediment free of organic matter</i>						
C1	0	No damage	0	No damage	0	0
C2	15	No damage	0	No damage	0	0
C3	50	Polyps inflation	20	No damage	0	8
C4	150	Polyps inflation	100	No damage	0	40
C5	250	Abrasion	90	Necrosis	10	96
C6	350	Abrasion	100	No damage	0	60
C7	450	Necrosis	100	No damage	0	180

### 3. Results

#### 3.1. Effect of sedimentation without organic matter on coral tissue and photosynthetic efficiency

##### 3.1.1. Susceptibility index ( $SI_{Mb}$ )

We found a strong and positive relationship between sedimentation rate and  $SI_{Mb}$  ( $F = 25.34$ ;  $F_{df} = 5$ ;  $r^2 = 0.80$ ,  $p = 0.004$ ; Fig. 1A) for the seven colonies exposed to sediment free of organic matter.

The tissue injuries observed in the corals, the respective percentages of affected colony areas, as well as the  $SI_{Mb}$  estimated for each colony are shown in Table 2. As mentioned in the Methods session, before the exposure to sediment all colonies had normal color patterns and no indication of tissue injuries. During the experiment, the stress caused by sedimentation produced different physical damages, such as polyp inflation, abrasion, smothering and necrosis.

Over the 45 days of exposure, the control colony ( $0 \text{ mg cm}^{-2} \text{ day}^{-1}$ ) and the colony exposed to  $15 \text{ mg cm}^{-2} \text{ day}^{-1}$  (PDL sedimentation rate according to Dutra et al. (2006) retained the appearance of healthy tissue. At the end of the experiment, only the colony exposed to the highest concentration of sediment ( $C7$ ,  $450 \text{ mg cm}^{-2} \text{ day}^{-1}$ ) died (Table 2).

##### 3.1.2. Photosynthetic efficiency

Quite unexpectedly, the sedimentation rate did not affect the  $\Delta F/Fm$  of *M. braziliensis* zooxanthellae after 45 days of exposure ( $F = 2.794$ ;  $F_{df} = 6$ ;  $r^2 = 0.359$ ;  $p = 0.1555$ ; Fig. 1B). The negative pattern shown by the best fit line of the linear regression model in Fig. 1B may be biased by a single value of  $\Delta F/Fm$  in the data set, more specifically the  $\Delta F/Fm$  of the colony exposed to  $350 \text{ mg cm}^{-2} \text{ day}^{-1}$ , and therefore may not represent a real tendency of negative relationship between the sediment input (free of organic matter) and the photosynthetic efficiency of *M. braziliensis* zooxanthellae. At the end of the experiment the

values of  $\Delta F/Fm$  ranged from 0.53 to 0.69 ( $n = 7$ ,  $0.59 \pm 0.025$ , mean  $\pm$  SD).

#### 3.2. Effect of sedimentation and organic matter on coral tissue and photosynthetic efficiency

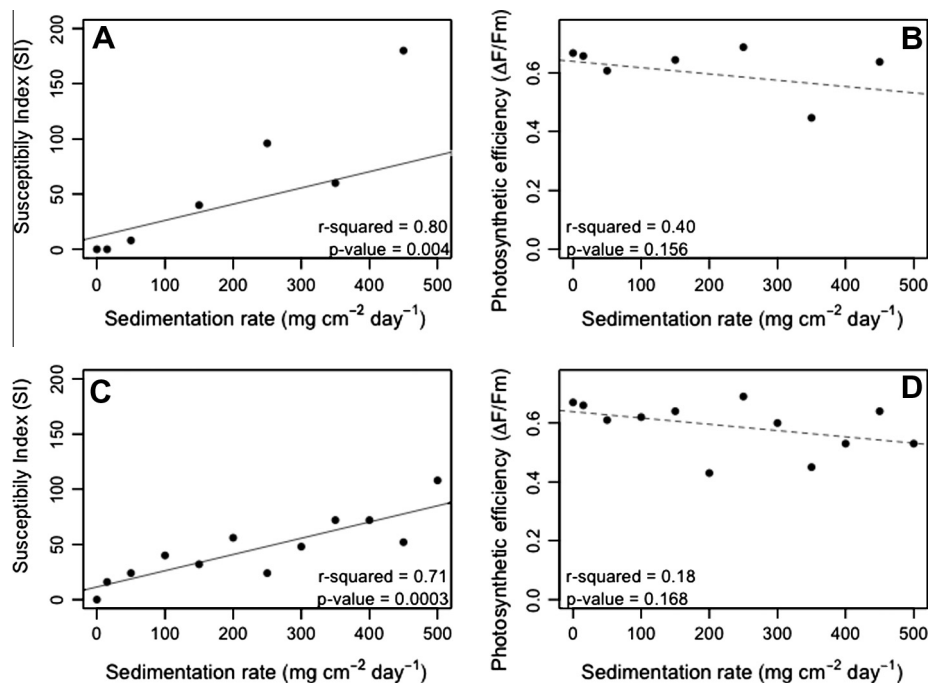
##### 3.2.1. Physical damage ( $SI_{Mb}$ )

After 120 h of exposure, there was also a positive relationship between sedimentation combined with organic matter and  $SI_{Mb}$  ( $F = 28.15$ ,  $F_{df} = 10$ ,  $r^2 = 0.7117$ , and  $p = 0.0003$ ; Fig. 1C). The injuries observed in the tissue of the 12 colonies are summarized in Table 3. At the end of the experiment only the control colony remained with a healthy tissue appearance and again the colony exposed to the highest concentration of sediment showed the highest value of  $SI_{Mb}$ .

##### 3.2.2. Photosynthetic efficiency

Again, the linear regression model of the *M. braziliensis* colonies exposed to sediment with organic matter did not show the expected negative effect of sedimentation over  $\Delta F/Fm$ , after 72 h of exposure ( $F = 2.204$ ;  $F_{df} = 11$ ;  $r^2 = 0.18$ ,  $p = 0.168$ ). In this second experiment, despite the absence of significance for this relationship, photochemical efficiency tended to decrease with increasing sedimentation associated with organic matter. This trend can be observed from the best-fit line calculated for the regression model (Fig. 1D). After 72 h of exposure values of  $\Delta F/Fm$  ranged from 0.43 to 0.69 ( $n = 12$ ,  $0.59 \pm 0.025$ ).

According to the nonparametric Mann–Whitney test, after 120 h of exposure, the colonies exposed to sediment and organic matter had a higher susceptibility index when compared to the colonies exposed to the treatment with sediment devoid of organic matter ( $p = 0.006$ ; Fig. 2). As shown in Table 4 the colonies exposed to sediment without organic matter presented  $SI_{Mb}$  ranging from 0, for the colony exposed to  $15 \text{ mg cm}^{-2} \text{ day}^{-1}$  (colony C2), to 16, for colonies C5 and C7 exposed respectively to  $250 \text{ mg cm}^{-2} \text{ day}^{-1}$  and

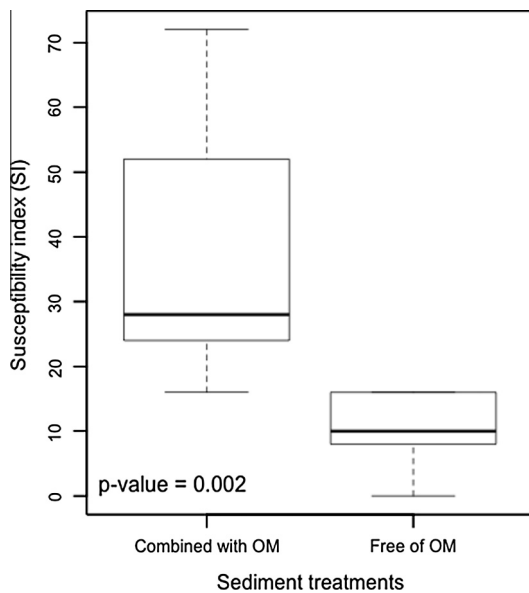


**Fig. 1.** Effects of long-term sedimentation, free of organic matter, on the susceptibility index of *Mussismilia braziliensis* (A) and the Photosynthetic Efficiency of *M. braziliensis* holobionts (B), and effects of short-term sedimentation, with organic matter, on the susceptibility index of *M. braziliensis* (C) and the photosynthetic efficiency of *M. braziliensis* holobionts (D).  $p$  values and  $r$ -squared of each linear regression are shown in each of the four scatter plots. Solid best fit lines of the regression models indicate the significance of the relationships and dashed best fit lines indicate non-significant relationships.

**Table 3**

SI calculated for each colony exposed to sediment with organic matter after 120 h of sedimentation exposure.

Colony	Sedimentation rate ( $\text{mg cm}^{-2} \text{day}^{-1}$ )	PD 1	AA (%)	PD 2	AA (%)	SI $\Sigma(\text{PD} \cdot \text{AA})$
<i>Colonies exposed to sediment and associated organic matter</i>						
C8	0	No damage	0	No damage	0	0
C9	15	Polyps inflation	35	No damage	0	16
C10	50	Polyps inflation	45	No damage	0	24
C11	100	Polyps inflation	95	No damage	0	40
C12	150	Polyps inflation	75	No damage	0	32
C13	200	Polyps inflation	5	Abrasion	80	56
C14	250	Polyps inflation	60	No damage	0	24
C15	300	Smothering	45	No damage	0	48
C16	350	Polyps inflation	20	Smothering	65	72
C17	400	Abrasion	45	Necrosis	10	72
C18	450	Abrasion	55	Smothering	15	52
C19	500	Necrosis	60	No damage	0	108



**Fig. 2.** Comparison between SI of colonies exposed to sediment combined with organic matter (OM) and colonies exposed to sediment free of OM. The sediment amounts and the time of sedimentation exposure used in both treatments were the same. *p* value for this comparison was equivalent to 0.006 indicating significant differences between treatments.

$450 \text{ mg cm}^{-2} \text{ day}^{-1}$  ( $10 \pm 6.0663$ , mean  $\pm$  SD). The  $\text{SI}_{\text{Mb}}$  of colonies exposed to sediment with organic matter, on the other hand, ranged from 16 (C9, exposed to  $15 \text{ mg cm}^{-2} \text{ day}^{-1}$ ) to 72 (C16, exposed to  $350 \text{ mg cm}^{-2} \text{ day}^{-1}$ ), with a mean and SD equal to 36.66 and 21.2289, respectively.

**Table 4**SI calculated for each groups of *M. braziliensis* colonies ( $n = 6$ ) after 120 h of exposition to the same concentrations ( $0, 15, 50, 150, 250, 350$  and  $450 \text{ mg cm}^{-2} \text{ day}^{-1}$ ) of sediment treatments, respectively devoid of organic matter and sediment combined with organic matter.

Colony	Sedimentation rate ( $\text{mg cm}^{-2} \text{day}^{-1}$ )	PD 1	AA (%)	PD 2	AA (%)	SI $\Sigma(\text{PD} \cdot \text{AA})$
<i>Colonies exposed to sediment free of organic matter</i>						
C2	15	No damage	0	No damage	0	0
C3	50	Polyps inflation	20	No damage	0	8
C4	150	Polyps inflation	20	No damage	0	8
C5	250	Polyps inflation	30	No damage	0	16
C6	350	Abrasion	20	No damage	0	12
C7	450	Polyps inflation	30	No damage	0	16
<i>Colonies exposed to sediment and associated organic matter</i>						
C9	15	Polyps inflation	35	No damage	0	16
C10	50	Polyps inflation	45	No damage	0	24
C12	150	Polyps inflation	75	No damage	0	32
C14	250	Polyps inflation	60	No damage	0	24
C16	350	Polyps inflation	20	Smothering	65	72
C18	450	Abrasion	55	Smothering	15	52

#### 4. Discussion

The literature indicates that sediment severely interferes in the energy balance of corals, reducing the photosynthetic production and increasing respiration (Fabricius, 2005; Riegl, 1995; Rogers, 1983, 1990). In the present study, under controlled laboratory conditions, neither the long-term (45 days) exposure to sediment without organic matter nor the short-term (5 days) exposure to sedimentation and organic matter affected the photosynthetic efficiency of *M. braziliensis* zooxanthellae ( $\Delta F/F_m$ ). However, these conditions significantly decreased the tissue integrity of *M. braziliensis* colonies, measured from their susceptibility index ( $\text{SI}_{\text{Mb}}$ ) to sedimentation.

Unlike many studies that associate increased sedimentation with a decrease in coral holobiont photosynthesis (Jones et al., 1999; Nemeth and Sladeczek-Nowlis, 2001; Phillip and Fabricius, 2003; Riegl and Branch, 1995; Weber et al., 2006), *M. braziliensis* did not bleach and kept its photochemical efficiency rates ( $\Delta F/F_m$  equivalent to 0.6, approximately) after the exposures of 72 h to sediment and organic matter and of 45 days to sediment free of organic matter. The absence of a negative relationship between photosynthetic efficiency and sedimentation rate is an indication of the photo-acclimation capacity of this Brazilian coral, which is subjected to markedly turbid environments (Suggett et al., 2012). Moreover, high values of photosynthetic efficiency for colonies exposed to sedimentation rates above  $200 \text{ mg cm}^{-2} \text{ day}^{-1}$  also indicate a high tolerance of this species to sedimentation, even when it was subjected to intense impacts caused by sedimentation and organic matter inputs. Colonies of *Montipora peltiformis*, an abundant foliose species in the Australian Great Barrier Reef, used by Phillip and Fabricius (2003), bleached and had levels of  $\Delta F/F_m$

below 0.1 after exposure for 36 h to  $151 \pm 37 \text{ mg cm}^{-2} \text{ day}^{-1}$  of sediment.

The tissue injuries observed are possibly associated with the increased energy consumption of the corals due to stress caused by both the increasing sedimentation and the input of organic matter. The redirection of energy to defense mechanisms against the deposited sediment, or the simple loss of energy promote a metabolic imbalance, which can compromise the individuals' fitness (Hodgson, 1993; Rogers, 1983, 1990). Polyp inflation possibly represents a coral defense mechanism that facilitates the removal of sediment deposited on the colony's surface (Lasker, 1980; Stafford-Smith, 1993; Erfteimeijer et al., 2012). Whereas, abrasion, smothering (as a consequence of burial), and necrosis, represent damages caused by the deposition of sediment and organic matter (when present). Physical damages in corals are common consequences on reefs exposed to high sedimentation rates (Cortés and Risk, 1985; Fabricius, 2005; Johnson and Carter, 1987; Phillip and Fabricius, 2003; Rogers, 1990; Erfteimeijer et al., 2012).

In conditions which aimed to simulate the naturally turbid environment of Brazilian marginal reefs (up to  $200 \text{ mg cm}^{-2} \text{ day}^{-1}$ ), where sedimentation rates exceed the limits that appear in the literature as acceptable for reef growth in healthy conditions (Dutra et al., 2006; Leão et al., 2006, 2008), the injuries observed in the colonies' tissue were less severe. On the other hand, under laboratory conditions that simulated natural or anthropogenic impacts (above  $200 \text{ mg cm}^{-2} \text{ day}^{-1}$ ) such as storm events or dredging, when resuspension can produce sedimentation rates of  $200\text{--}1800 \text{ mg cm}^{-2} \text{ day}^{-1}$  (Bak, 1978; Piniak, 2007; Rogers, 1990), tissue injuries were more severe. In our experiment, smothering and tissue necrosis were observed only above  $200 \text{ mg cm}^{-2} \text{ day}^{-1}$ , while in other studies this kind of damage was observed in corals exposed to lower concentrations of sediment, for shorter intervals, as seen by Phillip and Fabricius (2003), who observed smothering and necrosis in *M. peltiformis* colonies after exposure for 12–18 h, to  $151 \pm 37 \text{ mg cm}^{-2} \text{ day}^{-1}$ .

Unlike *M. peltiformis*, which presents a flattened shape that promotes sediment accumulation on the colony's surface, the characteristic hemispherical shape of *M. braziliensis* possibly facilitates the removal of accumulated sediment, which tends to be driven by gravity, granting an adaptive advantage for this species in environments marked by intense sedimentation. Perhaps this is the reason for the Brazilian coral fauna to be mainly represented by massive forms (Leão et al., 2003).

The susceptibility of *M. braziliensis* to sedimentation, assessed through the  $SI_{Mb}$ , was higher when sediment was combined with organic matter. Sediment with organic components tend to be even more harmful for corals (Bruno et al., 2003; Lapointe et al., 2004; Sawall et al., 2011; Umar et al., 1998; Weber et al., 2012). The presence of organic matter must reduce the cleaning capacity of corals because of its flocculating action that promotes the aggregation of fine sediment into larger particles. Flocculation can be further enhanced by the release of defensive mucus by corals (Piniak, 2007). Organic matter can also promote necrosis in corals through the proliferation of microorganisms, some of which cause coral diseases (Fabricius and Wolanski, 2000; Weber et al., 2012). The higher susceptibility of corals to sediment rich in organic matter is a haunting result considering the continuous growth of human populations and the consequent increase in coastal marine pollution associated with a higher input of organically enriched sediments (Haapkyla et al., 2011). Anthropogenic fluxes of organic matter from rivers into coastal waters are currently two or three times higher than before the industrial and agricultural revolutions, and now, these sources of pollution affect about 25% of coral reefs around the world (Burke et al., 2011; Howarth et al., 2011).

Lirman and colleagues (2008) studying Caribbean corals observed that two species of corals (that also occur in Brazilian reefs, as indicated by Neves et al. (2006), *Porites astreoides* and *Siderastrea siderea*, grew more when exposed for a month to sediment ( $53 \text{ mg cm}^{-2} \text{ day}^{-1}$ ) combined with organic matter (176.2 ppm N and 3.8 ppm P) than under the same sedimentation conditions without organic matter (10.3 ppm N and 2.1 ppm P). The authors justified that these corals have the ability to ingest organic particles, obtaining alternative sources of energy. The ability of corals to benefit from organic components of sediments has also been reported by Anthony (1999, 2000, 2006), Anthony and Fabricius (2000), Edinger et al. (2000) and Rosenfeld et al. (1999), who respectively observed an increase of energy reserves, growth rates, and the resilience of coral reefs in face of disturbances caused by sedimentation. Possibly in the present study the negative effects of organic matter, such as flocculation and microorganism proliferation, prevailed over the positive effects, such as nutritional gain. The balance between damages and benefits from the contact with sediment and organic matter depends on the frequency and intensity of the stress as well as the tolerance of the coral species (Lirman et al., 2008).

Rogers (1990) pointed out the importance of scientists recognizing the tolerance limits of corals to lethal effects caused by sediment exposure, and suggested that sedimentation rates equivalent to  $10 \text{ mg cm}^{-2} \text{ day}^{-1}$  are sufficient to compromise the vitality of corals. Dutra et al. (2006), studying the relationship between the sedimentation and the vitality of the Abrolhos reefs in Brazil, agreed with this author and concluded that rates greater than  $10 \text{ mg cm}^{-2} \text{ day}^{-1}$  could be considered critical to the health of the sampled coral communities. Loya (1976) suggested that rates above  $15 \text{ mg cm}^{-2} \text{ day}^{-1}$  are required to cause decline in coral reefs. The present study showed that damages in the tissue of *M. braziliensis* colonies are associated not only with sedimentation rate, but also depend on the presence or absence of associated organic components. In the presence of organic matter (approximately 10% of sediment content), short exposure (120 h) to  $15 \text{ mg cm}^{-2} \text{ day}^{-1}$  was sufficient to cause damage in the corals, such as polyp inflation. When exposed to  $15 \text{ mg cm}^{-2} \text{ day}^{-1}$  of sediment free of organic matter, corals did not have their tissue affected, even when exposed for a longer period (45 days).

This study therefore demonstrates the tolerance of the Brazilian endemic coral *M. braziliensis* to sedimentation in the absence of organic matter. On the other hand, the presence of organic matter in the sediment reduces this tolerance. Tolerance is an important mechanism for the survival of corals that enables the existence and development of reefs in the Brazilian coast, marked by intense and constant sedimentation (Leão et al., 2003). Indeed, the tolerance to sedimentation depends on the coral species in question, the type of sediment and organic matter content, sedimentation rate, and the exposure time to stress.

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