Coupling between microphytobenthic biomass and fiddler crab feeding

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ARTICLE INFO

ABSTRACT

Among the organic matter ingested by fiddler crabs, microphytobenthos is of fundamental importance because it is their main N source. Microphytobenthos abundance generally develop semilunar changes as the dynamics of tidal exposures and day-night cycle are not held constant across days, modifying the balance between growth and mortality. In this study we explored the coupling between temporal dynamics in microphytobenthos abundance and crab feeding activity. We measured the Chlorophyll a content in the 2 mm surficial sediment surrounding the burrows and the crab feeding activity over two semilunar cycles. Chlorophyll a and crab feeding activity showed biweekly cyclic dynamics. Crabs did not concentrate feeding activity around days with maximum abundance of microhytobenthos. This phase difference between both dynamics could be the result of the crab feeding impact, but a crab experimental exclusion showed that the temporal dynamics of Chlorophyll a content stayed unchanged when feeding activity was removed. Comparisons between fed and unfed sediment suggest that the feeding efficiency changes with tidal dynamic. Crabs achieved more than 50% of Chlorophyll a extraction during days of highest feeding activity, and less than 30% during days of low feeding activity or low microhytobenthos abundance. Furthermore, comparisons of fed sediment between consecutive days indicated that Chlorophyll a was completely replenished during days with high flooding tides, but partially replenished during days near neap tides. Environmental conditions affecting feeding efficiency may select crabs to concentrate feeding activity before days with the highest microhytobenthos abundance. The low feeding impact on microphytobenthos dynamics suggests that fiddler crabs would not control microhytobenthos abundance and thus unable to absorb the increasing eutrophication of studied estuarine areas.

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1. Introduction

Despite being important carbon reservoirs (Cook et al., 2009), most detritus produced and accumulated in intertidal mudflats are generally considered food poor or nutrient-limited (Valiela and Teal, 1979; Montague, 1980; Genoni, 1985; Rice, 1982; Tenore, 1983; Galvan et al., 2008. In these nutrient-limited systems, fluctuations in resource availability may cascade through the community and influence consumption rates and activity patterns of intertidal organisms (Daleo et al., 2005; DeAngelis et al., 1989). In addition, recurrent variations in the physical, chemical, and biological environment related to the day-night cycle and tidal inundation and exposure cycles (Newell, 1979) may limit the activity and behavior of intertidal organisms to small temporal windows (Barnwell, 1968; Doherty, 1978; Reinsel and Rittschof, 1995; Weinstein and Randi, 1998). Thus, given fluctuations in primary production may vary with both day-night and tidal cycles (Pinckney and Zingmark, 1991), whether consumers allocate their main foraging activity around moments of high quality and availability of food (Williams and Pilditch, 1997) is almost unknown.

Mobile intertidal organisms may adjust their behavior by anticipating environmental changes associated to the tidal and day-night cycles (Barnwell, 1968; Morgan and Christy, 1995; Skov et al., 2005; Thurman, 2004). There are evidences of the coupling between locomotion and foraging activity to tidal cycle in estuarine crabs (Aguzzi et al., 2004; Cannicci et al., 1999; Palmer, 1995; Webb and Brown, 1965; Williams and Naylor, 1969), polychaetes (Last et al., 2009), and filter feeding bivalves (Williams and Pilditch, 1997). In these aspects some intertidal species are known to exhibit exclusive nocturnal foraging cycles (e.g. *Sesarma reticulatum*, Seiple and Salmon, 1982; *Hydrobia ulvae*, Vieira et al., 2010) while others show exclusively diurnal foraging cycles (e.g. fiddler crabs Crane, 1975; De la Iglesia et al., 1994; but see Burkenroad, 1947; Powers and Cole, 1976;). However, the coupling of feeding activity to larger time-scale predictable changes in food availability is relatively unknown (but see Stillman and Barnwell, 2004).

Fiddler crabs are a group of almost 100 semi-terrestrial marine crab species within the genus *Uca* that inhabit salt marshes,

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mangroves, and sandy or muddy beaches (Crane, 1975). With some exceptions (i.e. *Uca panamensis,* Takeda and Murai, 2003) fiddler crabs are deposit feeders (e.g. Lopez and Levinton, 1987; Miller, 1961). Nevertheless, a high proportion of the organic matter that fiddler crabs ingest is refractory (i.e. of low digestibility; Kristensen, 1972), and thus, they dialy process large amounts (several times their weight) of sedimentary material (Lopez and Levinton, 1987). During foraging, fiddler crabs ingest the organic matter as well as the bacteria and microphytobenthos (Wolfrath, 1992) attached to, and/or located between sediment particles. Microphytobenthos is mainly composed by cyanophytas, euglenophytas, and both benthic and planktonic diatoms (Kanaya et al., 2008; Lopez and Levinton, 1987) which are likely to be the main nitrogen source for fiddler crabs (Botto et al., 2005; Kanaya et al., 2008; Lopez and Levinton, 1987; Rice, 1982). This protein reservoir is especially important in a nitrogen limited environment such as marshes and mudflats (Genoni, 1985; Montague, 1980; Rice, 1982; Tenore, 1983; Valiela and Teal, 1979).

Deposit feeders are usually non selective foragers (e.g. Taghon, 1982; Taghon et al., 1978; Weissburg, 1992, 1993) probably due to the small-scale unpredictable spatial variations in food quality inherent to marine sediments (Weissburg, 1992, 1993). However, it is known that microphytobenthic growth is not uniform along semilunar cycles (Pinckney and Zingmark, 1991; Shaffer and Onuf, 1985). This is because of differences in the total daily irradiance available for photosynthesis due to the superimposition of the tidal and day-night cycles (Pinckney and Zingmark, 1991). Thus, when dealing with the temporal distribution of food resources, predictable variations in food availability may affect feeding activity. Nevertheless, the mechanical constraints in the feeding apparatus of fiddler crabs (Miller, 1961) may imply different foraging efficiencies depending not only on food abundance but on other physiological factors such as temperature and water content, in some way all correlated with the semilunar cycle. Thus, whether crabs increase their feeding activity during periods of high microphytobenthos abundance may depend on whether foraging efficiency changes across the semilunar cycle.

In this work we studied the level of coupling between the temporal dynamics in microphytobenthos abundance and in feeding activity of crabs. We studied whether the feeding impact may control microphytobenthos abundance, and whether feeding activity may vary in relation to feeding efficiency and resource replenishment.

2. Material and methods

2.1. Study system

The study was conducted at the Mar Chiquita coastal lagoon (Argentina, 37º32' to 37º45' S and 57º19' to 57º26' W), a 46 km^2 body of brackish water affected by semidiurnal low-amplitude (< 1.5 m) tides (Perillo et al., 1999). The fiddler crab *Uca uruguayensis* Nobili (up to 15 mm carapace width) occurs in tidal flats of this lagoon above the mean high tide level, adjacent to the edge of cordgrass (*Spartina densiflora)* marshes (Bogazzi et al., 2001). Crabs dig burrows that they use as refuge during high tide, as shelter against predators, and as mating and molting sites. Density of burrows in this area ranges 10–30 cabs m^{-2} (Bogazzi et al., 2001). As many other temperate fiddler crabs (e.g. Powers and Cole, 1976; Salmon, 1965), *Uca uruguayensis* has seasonal patterns of surface activity. Crabs are active on the surface from mid September up to mid April, being almost inactive during winter due to the low temperatures (temperature ranges from −4 to15 °C). During warm months, crabs emerge from their burrows during diurnal low tide and feed on superficial sediments creating feeding areas around burrow openings (distinguishable as more or less circular sediment patches with a scraped surface). During nocturnal low tides crabs keep inside burrows without surface activity (De la Iglesia et al., 1994).

The present study was conducted within an intertidal area where this fiddler crab is the dominant species, without the occurrence of other deposit feeders and in which predation has been rarely seen (Spivak and Sanchez, 1992).

2.2. Co-occurring temporal dynamics

We studied the co-occurring temporal dynamics in the microphytobenthos abundance and in the feeding activity of crabs, from February to March 2009. Crabs fully engage in reproductive activities from mid November to mid or late January (Bogazzi et al., 2001). Thus, during the sampling period, crabs were not expected to engage in reproduction which may change the crab feeding activity time budgets.

At least every 2 days and during the minimum low tide period, we randomly selected 10 circular areas (0.78 m^2 each), each one delimited by an iron-ring (1 m diameter). The rings were kept in place throughout the day, and delimited areas were used for the observation of crab activity and for the quantification of microphytobenthos abundance.

Microphytobenthos abundance was estimated by quantifying the Chlorophyll *a* content (Magni et al., 2000) within the sediment that crabs process for feeding. Within each circular area and by using a syringe (13 mm diameter) we obtained three sub-samples of 2 mm depth that were pooled to yield one sample prior to analysis. We choose such depth for two reasons: (1) it is a standardized depth of the sediment euphotic zone (MacIntyre et al., 1996), and (2) it also corresponds to *U. uruguayensis*' foraging paths (P.R. pers. obs.). Samples were taken from unfed areas. Each sample was placed in a 50 ml falcon tube which was transported to the laboratory in conditions of dark and refrigerated conditions (0 °C) to minimize pigment degradation. Samples were processed to quantify the Chlorophyll *a* content during the following 24 h using the spectrophotometric method with acidification (Lorenzen, 1967). Chlorophyll *a* content was expressed as mg of Chlorophyll *a* cm^{-2} of sediment.

To explore the temporal dynamic of fiddler crabs feeding activity we observed crabs during daytime low tides. Each 30 minutes, from 3 hours before the low tide up to 3 hours after low tide we sequentially observed each of the 10 circular areas. The observation of each area took between 1–2 min, which was enough time to count the number of crabs feeding and/or involved in other activities (i.e. courting, fighting, burrowing). Counts were performed using 10x50 binoculars and at least 5 m far from the areas to avoid disturbing crabs' activity. For each circular area we calculated the mean number of feeding crabs across all censuses of each day. This value was used as an index of feeding activity by giving an estimator of the overall number of feeding crabs m^{-2} during the entire low tide period of crab activity.

To evaluate whether both Chlorophyll *a* content and the feeding activity of crabs have cyclic variations across days we used spectral analysis (Chatfield, 2004). In spectral analysis, by using the Fourier transform, a time series is decomposed into a spectrum of cycles of different lengths that can be expressed as a sum of sine wave components of different frequencies, amplitude and phase. Each sine wave component that is decomposed takes the following form:

$$amplitude \times Sine(t \times frequency \times 2 \times Pi + phase)$$

were *t* is the time unit (days) of the time series.

The spectral analysis gives the power spectrum function that can be interpreted as the variability of the time series distributed among different wave frequencies. Thus, the power spectrum allows the identification of the most important frequencies explaining the variability of the times series. Maximum Likelihood Ratio tests (Hilborn and Mangel, 1997) were employed to evaluate whether Chlorophyll *a* content and the feeding activity of crabs time series shared the same parameters (frequency, amplitude and phase) of the

most important sine wave component. Maximum Likelihood Ratio Tests were also used to construct confidence limits for the parameters.

Using the estimated phase values of the most important sine wave component of both times series we calculated the phase difference (PD) between them, in units of days, using the following equation:

$$PD = \frac{\left(Phase_{chlorophyll} - Phase_{crabs}\right) \times \left(Period_{chlorophyll} + Period_{crabs}\right) \Big/ 2}{360}$$

where Phase was in degrees and Period was in days. Bootstrap confidence limits (Manly, 2007) were constructed at the 95%.

2.3. Crab exclusion and microphytobenthos dynamics

To evaluate whether the phase shift between both dynamics (see results) is partly due to the foraging activity of crabs (i.e. through predation and/or sediment reworking) we compared the temporal dynamic in the Chlorophyll a content with and without crab activity. We delimited two areas (3 x 8 m each) with wood sticks on each corner. In one of these areas we extracted all crabs by using a squeeze bottle to carefully pump water inside crabs' burrows and capturing them when surfacing. Each captured crab was transported to an area 50 m far from experiments and given an artificial 10 cm depth hole (1 cm diameter made with a pen), that was accepted as initial refuge and structure for digging new burrows. This extraction method generated an area free of crabs without disturbing sediment and without the presence of artificial boundaries (i.e. cages), that would modify the dynamics of sediment transport. However, the open area had the risk of continuous settlement of new crabs for which we did periodical visits (at least each 2 days) in order to remove each new crab within the area.

To quantify Chlorophyll a content, at least every 2 days we obtained 10 sediment samples from each area during the minimum low tide period. Using 10 x 50 binoculars and at least 5 m far from the areas, we counted the total number of crabs observed feeding in order to have an estimation of crab activity on both areas. Additionally we noted the number of males in courtship to have an estimation of the crab reproductive activity. Sediment samples were collected and processed as in Section 2.2. We performed spectral analysis for both Chlorophyll a content time series to identify cyclic variations across days (Chatfield, 2004). We performed Likelihood Ratio Tests (Hilborn and Mangel, 1997) to evaluate whether parameters (frequency, amplitude and phase) of the most important sine wave component were the same with and without crab activity.

2.4. Immediate effect of feeding

We studied the feeding impact of crabs in order to evaluate their potential effect on microphytobenthos dynamics. As feeding activity showed temporal variations, the feeding impact may also be expected to vary across days. For this reason, and based on the co-occurring temporal dynamics (se results) we measured the feeding impact at four different semilunar activity state of crabs: (1) MIA, morning intermediate activity of crabs, corresponding to low tides occurring between 7–9 Hs, (2) HA, high activity of crabs, corresponding to low tides occurring between 11–13 Hs, (3) AIA, afternoon intermediate activity of crabs, corresponding to low tides occurring between 15–17 Hs, and (4) LA, low activity of crabs, corresponding to low tides occurring between 19–21 Hs. During LA days it is also possible the occurrence of a very early morning low tide. However, as there is only between 2–3 hs of sun light (especially in summer) before the ebbing tide covers the sediment, crabs develop surface activity during the following afternoon-evening low tide (i.e. corresponding to AIA).

For each of the four semilunar activity states of crabs, and between three and four hours before low tide (before crabs initiate feeding) we

randomly selected 20 recently open burrows. Chosen burrows were between 5–6 m apart. In ten of these burrows we plugged the entrance using spherical lead weights to prevent the inhabiting crab from emerging and feed on the surrounding sediment. One hour after low tide we obtained sediment samples to quantify Chlorophyll a content. Samples were taken within the 5–10 cm radius from the opening. From open burrows in which crabs were allowed to feed, we obtained samples of fed and unfed sediment (OF and OU, respectively). From plugged burrows, we obtained samples from unfed sediment (PU). Unfed sediment samples were taken by using a syringe (13 mm diameter) and extracting three sub-samples of 2 mm depth that were pooled to conform each sample. Fed sediment samples were taken by collecting feeding pellets within 3 circular areas demarcated with a syringe (13 mm diameter). The spectrophotometric method with acidification (Lorenzen, 1967) was used to quantify the Chlorophyll a content. Because fed and unfed samples were collected from physically different structures, we measured the wet weight of each sample (to the near mg) and expressed the Chlorophyll a content as mg of Chlorophyll $a \, g^{-1}$ of sediment. A two-way ANOVA was used to compare Chlorophyll a content in relation to sediment type (OF, OU, PU) and semilunar activity state of crabs (LA, MIA, HA, AIA).

We evaluated the feeding (FI) impact as the proportion of Chlorophyll a that decreased due to feeding. For each unplugged burrow we calculated the feeding impact with the following equation:

$$FI = \frac{Chl_{OU} - Chl_{OF}}{Chl_{OU}}$$

where Chl_{OU} is the Chlorophyll a content in OU samples and Chl_{OF} the Chlorophyll a content in OF samples. An ANOVA was used to compare the feeding impact between semilunar activity state of crabs (LA, MIA, HA, AIA).

2.5. Feeding impact and tidal dynamics

We evaluated whether the decrease in Chlorophyll a content due to feeding in a determined area may persist the following day. For each of the 4 semilunar activity states of crabs and between three and four hours before low tide (before crabs initiate feeding) we randomly selected 20 recently open burrows (different burrows to the section 2.4). In ten of these burrows we plugged the entrance using spherical lead weights to prevent the inhabiting crab from emerging to feed on the surrounding sediment. Then, one hour after low tide using wood sticks we marked fed and unfed sediment areas (OFA and OUA, respectively) from burrows in which crabs were allowed to forage, and unfed areas (PUA) from burrows in which we plugged the opening. The following day between three and four hours before low tide we located all marked areas (OFA, OUA and PUA) and plugged the burrow entrances. With this procedure we obtained unfed sediment that had either been processed by crabs the previous day (OFA) or not (OUA and PUA). One hour after low tide we obtained samples from each of the marked areas. A two-way ANOVA was used to compare Chlorophyll a content in relation to sediment type (OFA, OUA, PUA) and semilunar activity state of crabs (LA, MIA, HA, AIA).

To evaluate whether the Chlorophyll a content was replenished the following day within fed sediment areas we performed an indirect estimation using data from sections 2.4 and 2.5. The following equation was used to calculate the mean proportion of consumed Chlorophyll a that was replenished the following:

$$CR = \frac{(Chl_{OFA} - Chl_{OF})}{Chl_{OU} - Chl_{OF}}$$

where Chl_{OFA} is the mean Chlorophyll a content in OFA samples, Chl_{OF} the mean Chlorophyll a content in OF samples, and Chl_{OU} the mean Chlorophyll a content in OU samples.

3. Results

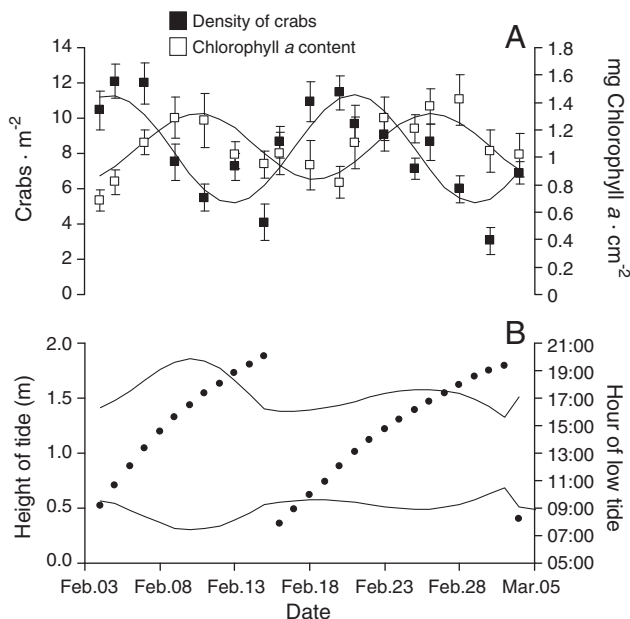### 3.1. Co-occurring temporal dynamics

During the study 91 % of observed crabs were observed feeding. The rest were involved in other non-reproductive activities such as burrow maintenance/construction (3 %), and fighting (6 %). During this sampling no males were observed in courtship activities.

The crab feeding activity and the Chlorophyll *a* content of the upper 2 mm surficial sediment (Fig. 1) showed cyclic changes across time. The crab feeding activity showed maximum values during days in which low tide occurred between 10:00–13:00 hs, while Chlorophyll *a* content showed maximum values during days in which low tide occurred between 15:00–17:00 hs (Fig. 1).

The power spectrum analysis found that the cyclic pattern in the feeding activity of crabs and in the Chlorophyll *a* content could be explained by sine waves of 16.17 and 15.52 days period, respectively (Table 1). Likelihood Ratio Tests indicated that the sine wave component of times series had the same frequency but different amplitude and phase (Table 1 and 2). The phase difference between both time series was 5.76 days (95% Bootstrap confidence limit: 4.26, 7.42).

3.2. Crab exclusion and microphytobenthos dynamics

The exclusion of crabs from the experimental area could successfully maintain an area free of crab activity (Fig. 2). The initiation of reproductive season was evidenced by the increase of courtship activity at the end of the experiment. Chlorophyll *a* content of the upper 2 mm surficial sediment from areas with and without crab activity showed cyclic changes across time (Fig. 2), which could be explained by one Sine wave component (Table 4). Crab feeding activity did not significantly influence temporal patterns in Chlorophyll *a* content in sediment; both time series had the same frequency, phase and amplitude (Likelihood Ratio Tests: $\chi^2 = 0.85$, df = 3, p = 0.8365).

Table 1
Parameters for the most important sine wave component from the spectral analysis applied to feeding activity of crabs and Chlorophyll *a* content. Period was obtained from frequencies values (period = 1 / frequency).

	Mean		95% Confidence limit	
	Feeding activity	Chlorophyll *a*	Feeding activity	Chlorophyll *a*
Frequency	0.0618	0.0644	0.0594, 0.0682	0.0601, 0.0693
Phase	1.2691	-1.1059	1.0120, 1.5290	-1.5385, -0.6403
Amplitude	3.0806	0.2433	2.3134, 3.7979	0.1302, 0.3483
Period	16.17	15.52	14.67, 16.83	14.43, 16.63

3.3. Immediate effect of feeding

The Chlorophyll *a* content of sediment differed in relation to both sediment type and semilunar activity state of crabs (Table 3A). Chlorophyll *a* abundance of unfed sediments from plugged and unplugged burrows was similar; but higher from sediment collected from fed areas (Fig. 3). The feeding impact of crabs differed between semilunar activity states of crabs (ANOVA: $F_{3,36} = 16.21$, p < 0.0001, MSE = 0.0191, Fig. 4). Crab feeding impact was highest during days of maximum crab activity (HA) corresponding to days where low tides occurred near midday and Chlorophyll *a* content showed intermediate values. Crab feeding impact was lowest during days in which Chlorophyll *a* content was minimum (MIA days; Fig. 4).

3.4. Feeding impact and tidal dynamics

The Chlorophyll *a* content in sediment differed between semilunar activity states but did not differ between areas that were fed (OFA) or not fed (OUA and PUA) the previous day (Table 3B; Fig. 3). However, the Chlorophyll *a* content replenishment estimations indicated that during days near neap tides (LA and MIA) Chlorophyll *a* content was partially replenished between consecutive days (proportions of Chlorophyll *a* replenished: 0.68, 0.28, for LA and MIA days respectively). On the contrary, during days with higher flooding tides (HA and AIA) Chlorophyll *a* content was completely replenished between consecutive days (proportions of Chlorophyll *a* replenished: 1.14 and 1.11 for HA and AIA days, respectively).

4. Discussion

Most work on rhythmic patterns of estuarine organisms have examined locomotor and feeding activity within a tidal cycle (e.g. Aguzzi et al., 2004; Cannicci et al., 1999; Palmer, 1995; Webb and Brown, 1965; Williams and Naylor, 1969; Williams and Pilditch, 1997), and reproductive timing along semilunar, lunar and longer-

Fig. 1. (A) Time series for the density of feeding crabs (filled boxes) and for the Chlorophyll *a* content in sediment (open boxes). The lines indicate the expected values from the fitted model. (B) The tidal cycle. The lines indicate the height of the diurnal low tide (during which crabs are active), and the height of the high tide before the diurnal low tide. Dots indicate the hour at which the diurnal low tide occurred.

Table 2
Likelihood Ratio Tests comparing the parameters for the sine wave components of feeding activity and Chlorophyll *a* content time series. P-values < 0.05 indicate that assuming similar values for a determined parameter implies a significant loss in the variability explanation of the time series, that is measured as an increment in the negative log likelihood (NLL). The NLL for the "Different sine wave components" hypothesis is the sum of the NLL of the both time series fitted separately. The NLL for the "Same frequency" hypothesis is the sum of the NLL of the both time series with the restriction that both are fitted with the same value for the frequency parameter. The regarding "Same frequency and amplitude" and "Same frequency and phase" hypotheses follow the same basis scheme, and their NLL are contrasted with the one for "Same frequency" in order to evaluate whether to estimate different amplitude or phase values for each series improves significantly the variability explanation of the time series.

	NLL	χ^2	Parameters	df	p
Different sine wave components	536.26		6		
Same frequency	536.49	0.4546	5	1	0.5002
Same frequency and amplitude	543.99	15.0176	4	1	0.0001
Same frequency and phase	573.19	58.3812	4	1	<0.0001
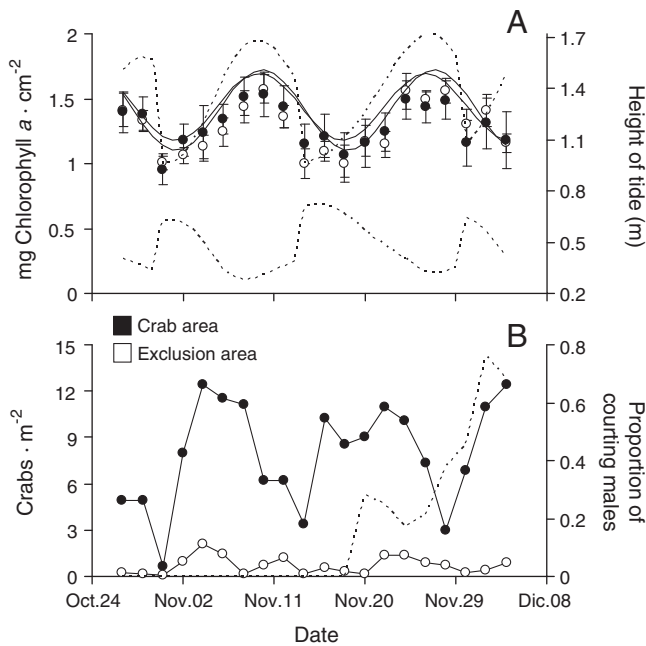
Fig. 2. (A) Time series for the Chlorophyll *a* content per cm² of sediment with crab activity (filled circles) and of sediment with crab exclusion (open circles). Solid lines indicate the expected values from the fitted models. Dotted lines indicate the height of the diurnal low tide (during which crabs are active), and the height of the high tide before the diurnal low tide. (B) Density of crabs from the area with crab activity (filled circles) and from the area with crab exclusion (open circles). Dotted line indicates the proportion of male crabs that were engaged in courtship.

period cycles (e.g. Christopher et al., 2008; Morgan and Christy, 1995; Skov et al., 2005). In this work, we explored the temporal pattern of a non-reproductive behavior within a time scale larger than the tidal cycle. Our results showed that both feeding activity of the fiddler crab *Uca uruguayensis* and the abundance of microphytobenthos fluctuated across days with cycles of nearly 15–16 days period. Contrary to the expected, crabs did not concentrate feeding during days of highest Chlorophyll *a* content. Instead, feeding activity occurred mainly 5–6 days before the maximum for the Chlorophyll *a* content, indicating a phase difference between both dynamics.

The phase difference between feeding activity and Chlorophyll *a* content may represent a time shift due to the consumption impact of crabs. Consistent with other studies (e.g. Dye and Lasiak, 1986; Hoffman et al., 1984; Reinsel, 2004; Wolfrath, 1992) the experimental comparisons between fed and unfed sediments showed that, at the

Table 3
Summary statistics for the two-factors ANOVAs comparing the Chlorophyll *a* content between sediment type (unfed sediment from plugged burrows, unfed and fed sediment from unplugged burrows) and semilunar activity state of crabs (low activity, morning intermediate activity, high activity, and afternoon intermediate activity of crabs). (A) correspond to samples with feeding impact of the day (Section 2.4), and (B) correspond to samples with feeding impact of the previous day (Section 2.5). Data was square root transformed.

|	MS	df	F	p
(A) Feeding impact of the day				
Sediment type	0.4218	2	13.63	<0.0001
Semilunar activity state	0.1216	3	3.93	0.0105
Sediment type X Semilunar activity state	0.0230	6	0.74	0.6147
Error	0.0309	108		
(B) Feeding impact of the previous day				
Sediment type	0.0110	2	0.26	0.7723
Semilunar activity state	0.3488	3	8.20	<0.0001
Sediment type X Semilunar activity state	0.0081	6	0.19	0.9790
Error	0.0425	108		

Table 4
Parameters for the most important sine wave component from the spectral analysis applied to the Chlorophyll *a* content with and without crab activity. Period was obtained from frequencies values (period = frequency⁻¹).

	Mean		95% Confidence limit	
	With crab activity	Without crab activity	With crab activity	Without crab activity
Frequency	0.0588	0.0605	0.0558, 0.0162	0.0563, 0.6482
Phase	2.8621	2.6958	2.4457, 3.2786	2.1091, 3.2824
Amplitude	0.2324	0.1905	0.1774, 0.2875	0.1328, 0.2482
Period	16.99	16.52	16.16, 17.93	15.43, 17.77

small scale (i.e. square centimeter), crabs may decrease up to 60% of the Chlorophyll *a* content of the sediment that they process during days of high activity. This consumption impact suggests that temporal changes in the activity of crabs' feeding may potentially shape the temporal changes in the abundance of Chlorophyll *a* content. Nevertheless, the overall decrease in the Chlorophyll *a* content of the mudflat would depend on the proportion of consumed sediments. In this vein, the experimental exclusion of crabs within a large area showed that the presence or the absence of the feeding activity of crabs did not imply a change in the temporal dynamics of Chlorophyll *a* content. Thus, the feeding impact of crabs at the small scale is not necessarily transferred to the large scale, where other factor may prevail over the effect of crabs' feeding. On the other hand, Chlorophyll *a* dynamics seem to be directly associated to the tidal dynamic. Indeed, maximum values of Chlorophyll *a* content (Fig. 1A and Fig. 2A) co-occur with maximum tidal amplitude (i.e. the difference between the high and low tide height in Fig. 1B and Fig. 2B). This pattern suggests that cyclical dynamics in the Chlorophyll *a* content may be mainly driven by tidal dynamics.

Conceptual mathematical models (see Blanchard et al., 2001; Guarini et al., 2000; Serôdio and Catarino, 2000; Spilmont et al., 2007) suggest that during daytime exposures microphytobenthos biomass increases in the uppermost centimeter of the sediment due to photosynthesis. Such growth exceeds natural mortality and grazing by deposit-feeders (Blanchard et al., 2001; Guarini et al., 2000; Serôdio and Catarino, 2000). During nighttime exposures microphytobenthos does not photosynthesize and thus decreases in biomass due to natural mortality and grazing by deposit-feeders. During immersions biomass also decreases due to resuspension into the water column. Thus, the succession of exposures and immersions, originates a series of within day oscillations in the balance between growth and mortality, shaping short-term dynamics of microphytobenthos biomass (Blanchard et al.,
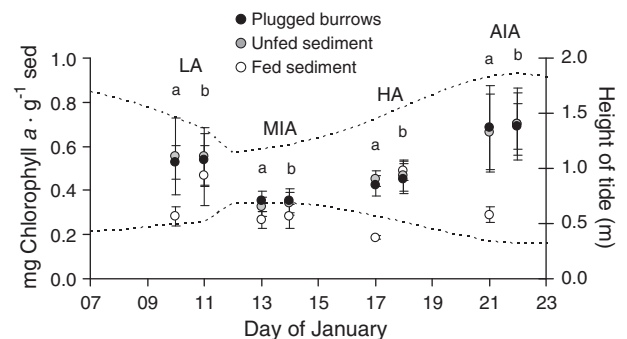
Fig. 3. Mean (points) and standard error (whiskers) for the Chlorophyll *a* content per g of unfed sediment from plugged burrows (filled circles), unfed (gray circles) and fed (open circles) sediment from unplugged burrows. Samples were collected during days with low activity (LA), morning intermediate activity (MIA), high activity (HA) and afternoon intermediate activity of crabs (AIA). The dotted lines show the height of the diurnal low tide (during which crabs are active), and the height of the high tide before the diurnal low tide. Lowercase a denotes samples from Section 2.4 and lowercase b denotes samples from Section 2.5.
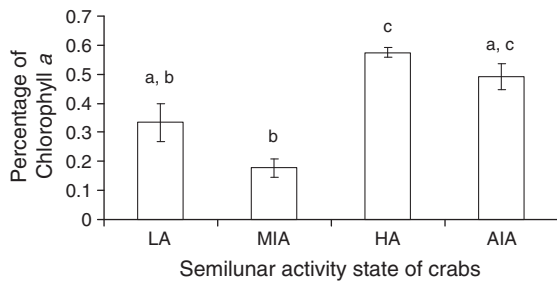
Fig. 4. Feeding impact as the mean proportion (open bars) and standard error (whiskers) of the Chlorophyll *a* content that was decreased by the feeding activity. Same letter indicates non significant differences after Tukey multiple comparisons.

2001; Guarini et al., 2000). The models also predict the balance between growth and mortality rates to vary between days; as the combination of exposures and daytime is not held constant across days due to a phase difference between the daytime cycle (24.0 hs) and tidal cycle (24.8 hs). Therefore, spring tides with higher exposition time would yield higher increments in microphytobenthos biomass than during neap tides with lower exposition time due to shorter tidal amplitude. In our data, the fortnightly frequency oscillation with peaks of Chlorophyll *a* content during spring tides suggests the balance between growth, mortality and resuspension rates varies across days. Nevertheless, it is interesting that during our sampling period the low spring tides did not occur at midday as they did in sites for which the tested models were constructed (see Guarini et al., 2000). Therefore, higher increments in Chlorophyll *a* during spring tides may be associated with the proportional time that the areas are exposed rather than to the level of light intensity. In fact, during midday excessive incident irradiance (Kingston, 1999) and high temperature and desiccation stress (Admiraal, 1977; Pinckney and Zingmark, 1991) may decrease the photosynthetic rate due to downward migration away from photoinhibitory light levels. Thus, tidal dynamics through changes in irradiance, sediment temperature and desiccation could explain the observed pattern in the temporal dynamics in the Chlorophyll *a* content.

In systems where food availability changes predictably through time, consumers could be more likely to evolve mechanisms that optimize resource utilization. In this aspect, any mechanism allowing crabs to anticipate the environmental changes in food availability and/ or quality would be adaptive (Barnwell, 1968; Thurman, 2004; Yerushalmi and Green, 2009). Our results showed that food abundance was quite predictable in time; however, crabs did not concentrate feeding activity around days of highest microphyto-benthos abundance. Three main possible scenarios may account for the uncoupling between microphytobenthos abundance and feeding activity cycles: (1) temperature constraints, (2) mechanical con-straints, and (3) reproductive entrainment. (1) The phase difference between cycles could be due to a shift between days with the highest abundance of microphytobenthos and days with the best temperature conditions for crab activity (e.g. Pascal et al., 2008; Przeslawski et al., 2009). Surface temperatures above 40 º C have lethal effects on crabs (Edney, 1961; Wilkens and Fingerman, 1965). Thus, changes in air and sediment temperature during daytime may affect feeding activity (e.g. Edney, 1961; Nakasone, 1982; Smith and Miller, 1973; Wilkens and Fingerman, 1965). During low tides occurring before midday heat gain of surface sediment rarely exceeds 30 °C (see Bortolus et al., 2002), which is a non dangerous thermal condition for crab activity (Edney, 1961; Wilkens and Fingerman, 1965). On the contrary, especially during hot days and low tides occurring after midday, surface sediment gains considerable heat (more than 45 º C; see Bortolus et al., 2002); which may force crabs to avoid surface activity. Therefore, uncoupling between microphytobenthos abundance and feeding activity cycles may partly result from higher abundances of microphytobenthos occurring during days with high probability of

lethal temperatures for crabs.(2) The thermal and desiccation conditions may also affect the performance of the feeding apparatus. During the feeding process (see Miller, 1961), crabs use the minor cheale to scrape the surficial sediment and bring into the buccal cavity particles with detritus, algae and bacteria. Once there, the action of maxillipeds scour off the attached organic matter and discard the coarser and clean grain particles. To carry out this sorting process, crabs employ a flotation sorting mechanism which introduces water into the buccal cavity to float light food holding it between mouthparts (Miller, 1961). Heavier particles are precipitated and discarded, for which only light food particles are allowed to pass into the mouth. Thus, even if food source is abundant, under water shortage the flotation mechanism will not successfully sort food particles (Miller, 1961). In general, during the spring low tides water content in sediment is very low, given the extended time areas are uncovered and under sun irradiation (pers. obs.). In this way, the availability of food would depend not only on the growth of microphytobenthos but on the availability of water for the operation of the flotation mechanism. Finally, (3) when crabs are reproductively active, they synchronize mating activity with semilunar cycles (e.g. Christopher et al., 2008; Morgan and Christy, 1995; Skov et al., 2005), showing also high mating activity during days of high feeding activity (see Ribeiro et al., 2010). It is likely that the entrainment of reproduction with semilunar cycles is achieved by the synchroniza-tion of all crab activity. Thus, the uncoupling between microphyto-benthos abundance and feeding activity may be the result of a general activity rhythm synchronized with semilunar cycles, and which persists even when crabs are not reproductively active.

Experimental studies (Lopez and Levinton, 1987; Robertson and Newell, 1982a, b; Weissburg, 1992, 1993) on other fiddler crabs species showed that feeding rate is positively correlated with food concentration. However, food extraction of ingested particles is inversely related to the feeding rate. This is because a large number of particles within buccal cavity saturate the flotation sorting mechanism (Robertson and Newell, 1982a; Weissburg, 1992). Thus, if crabs increased particle intake due to low food concentration, they would saturate the flotation sorting mechanism, decreasing the feeding efficiency. Under low feeding efficiencies the net energy gain could be in shortage for the metabolic demands of feeding, turning it into a costly activity (Weissburg, 1993). Thus, changes in the feeding efficiency could determine when to start and stop feeding (Robertson and Newell, 1982a; Weissburg, 1992, 1993). Overall, changes in food abundance and changes in environmental conditions may result in changes in the feeding efficiency, which may determine feeding activity. The experimental results on fed and unfed sediment showing highest Chlorophyll *a* extraction during HA and AIA days, could be due to better environmental conditions (low temperature and desiccation stress) and higher microphytobenthos abundances, respectively, than during LA and MIA days. Furthermore, although no significant differences were found for the Chlorophyll *a* content between sediment types containing the feeding impact of the previous day (results of Table 3B), the proportions of Chlorophyll *a* replenishment suggest that the replenishment of microphytobenthos between consecutive days is likely to be of 100% for HA and AIA days (i.e. before and during spring tides), and for LA days and low for MIA days. Thus, tidal dynamics seems to be essential for the replenishment of the microphytobenthos within an area that was processed and exploited by crabs. In this way, high feeding efficiencies plus high resource replenishment during HA and AIA days would select crabs to concentrate feeding activity around such days; while low feeding efficiencies and low resource replenishment during LA days would select crabs to decrease feeding activity around such days.

Given the increasing anthropogenic impact on estuarine areas, the development of mitigation policies to preserve and restore these areas may go hand in hand with identification and understanding of the mechanisms that can absorb eutrophication. In particular, when crabs

consume microphytobenthos, primary production becomes secondary production. However, our study suggest that fiddler crabs would not exert an important control on primary production, as Chlorophyll *a* showed temporal dynamics unaffected by the feeding activity of crabs. Furthermore, a study of secondary production in a population of *Uca uruguayensis* reports yields of no more than 0.5 mg of crab · cm⁻² · year⁻¹ (Armendáriz and César, 2006). Although, in the present study we have not directly measured productivity, our estimations of Chlorophyll *a* content would suggest a surplus of primary production that is not being incorporated by crabs as secondary production. Thus, the low feeding impact on microphytobenthos dynamics suggests that fiddler crabs would not be able to absorb the increasing primary production (e.g. eutrophication).

Acknowledgements

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