

# Effect of “Whitemouth Croaker” (*Micropogonias furnieri*, Pisces) on the Stability of the Sediment of Salt Marshes—an Issue To Be Resolved

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**Abstract** Among the predators, fish are prevalent in intertidal soft-bottom zones, and many create substantial interruptions in the sediment surface through their feeding, thus affecting the movement of fluids in the sediment-water interface and therefore the rates of deposition and local erosion. This study was designed to determine whether or not *Micropogonias furnieri*—an ecologically significant benthophagic southwestern Atlantic Ocean predator—modified erosion and/or sedimentation processes in salt marshes. The results indicated that this species exhibited a preference for areas without vegetation cover at the time of feeding since a greater abundance of pits was found in those environments. Moreover, the volume analysis of the pits in the two areas indicated that the size of the fish that had foraged in the sediment was significantly larger

in the nonvegetated areas. The results of the *M. furnieri*-exclusion experiment indicated that the presence of this sciaenid neither resulted in a decrease in benthic organisms in the nonvegetated areas nor affected the vertical distribution of the infauna. When *M. furnieri* was excluded, the sediment exhibited higher critical-shearing and frictional-velocity values than in areas where *M. furnieri* had access and therefore was less likely to be eroded. The data from these experiments enabled us to conclude that the foraging action of *M. furnieri* modified the stability of the sediment as a result of the predatory pressure that the fish exerted on the organisms inhabiting the salt marshes, thus resulting in the generation of elliptical depressions. That modification of the sediment stability was evidenced in two principal ways: (i) a negative effect on the microphytobenthic organisms that decreased the concentration of extracellular polymeric substances in the sediment and (ii) an increased roughness of the bottom and increased percentage of sand in the particle composition of the sediment, where the fish had foraged.

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## Introduction

Salt marshes are extremely productive habitats, where the high secondary production of the benthos (Wong et al. 2011) provides abundant food resources for fish and macrocrustaceans at high tide, essential foraging grounds for waterfowl during all tides, and use by wading birds, insects, and mammals at low tide (Luo et al. 2015; Palomo et al. 2003; Martinetto et al. 2005). The impact of predation depends on the sediment type among other conditions (Seitz et al. 2001) and should affect

benthic organisms as well as the sediments themselves (Molina 2013). Furthermore, birds and epibenthic predators may influence the zonation (Hiddink et al. 2002), depth distribution (Esselink and Zwarts 1989; Quijón and Jaramillo 1996), life history (Hilton et al. 2002), and size structure (Botto et al. 2000; Heck and Valentine 2007; Martinetto et al. 2005) of the prey population.

Predation is a key mechanism in structuring and maintaining diversity and stability in aquatic communities (Chesson 2000). Among the predators, fish are prevalent in intertidal soft-bottom zones (Norton and Cook 1999). The infauna are major components of the diets of those fish, with some species feeding exclusively on certain prey (Little 2000). At least two general types of epibenthic predators or predation mechanisms can be found in soft-sediment environments: first, the so-called *prey-nipping* type, such as the sole (*Paralichthys orbignianus*) or the silverside (*Odontesthes argentinensis*), with those fish using visual or olfactory stimuli to detect the exposed infauna (De Groot 1971), and second, the *sediment-biting* type or burrowing predators, comprising benthivorous fish, such as the rays and the whitemouth croaker, *Micropogonias furnieri* (Hozbor and Garcia dela Rosa 2000), which not only deplete the adult infauna but also eat the larvae, the juveniles, and the more surface-oriented meiofauna that inhabit the first 2 in. of sediment (Smith and Coull 1987; Olsson et al. 2013; Mendoza-Carranza and Vieira 2007); although, it is necessary to clarify that almost always only small juvenile sediment-biting fish have the ability to retain meiofauna size prey in the sediment, and different life stages of the same fish could be predators on different size groups of benthos, i.e., the case of the spot *Leiostomus xanthurus*, where larval and postlarval spot (which have a terminal mouth) are planktivorous feeders, spot of 21–32 mm are benthic-feeding juveniles (due to metamorphose have a subterminal mouth) and filter meiofauna out of mouthfuls of sediment, and juvenile spot <50 mm feeds almost exclusively on meiofauna while spot >50 mm also feed on macrobenthos (Chestnut 1983; Ellis and Coull 1989).

A common feature of many soft-bottom predators is that they create substantial interruptions in the sediment surface through their feeding behavior and generate structures such as pits or burrows (Hall 1994). Within a slightly wider context, changes in the physical environment that are generated by these activities can conceivably produce migrations of the species that inhabit these disturbed areas (organisms coming into or leaving the disturbed area either through the water column or through the sediment; Molina 2013).

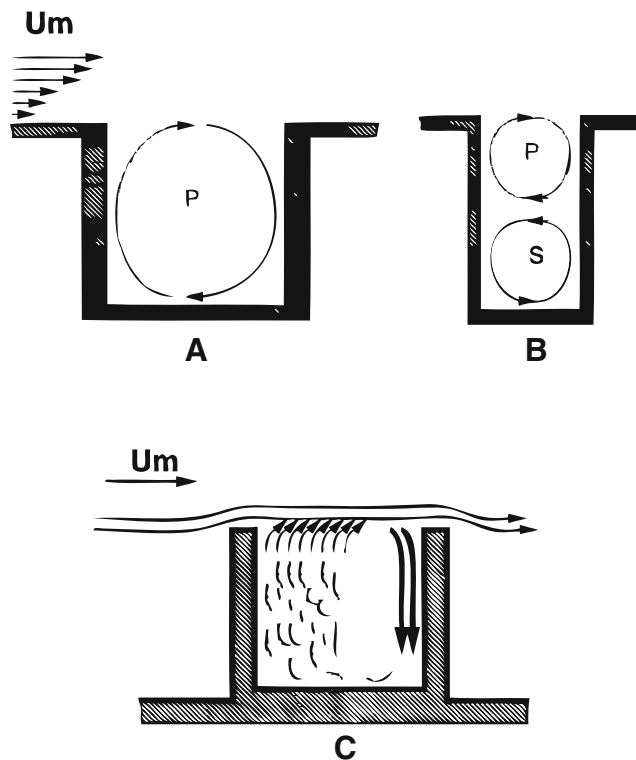
These newly generated conditions may also physically affect the movement of fluids across the sediment-water interface and therefore the rates of deposition and local erosion (Nowell and Jumars 1984; Self et al. 1989). A depression, for example, has an effect qualitatively opposite to that of an object protruding from the surface of the

sediment (Nowell and Jumars 1984; Abelson and Denny 1997) in increasing the cross-sectional area over which the current must distribute itself: the flow accordingly slows down upon passing over and within the depression. Therefore, the depressions in the sediment are areas of low shear stress in which the residence time of materials in suspension becomes greater (Nowell and Jumars 1984; Abelson and Denny 1997). As the velocity decreases, a pressure gradient is generated in the opposite direction that results in a flow separation involving a passage directly over the surface of the depression and a vertical drop within the cavity (Yager et al. 1993; Fig. 1c). The maximum tangential velocity of the vortex within depressions is approximately one tenth of the flow rate and does not exceed two tenths of the velocity of the main stream (Varzaly 1978; Sinha et al. 1982). Periodically, the vortex within the cavity may become unstable and then sink into the cavity. This vortex also replaces the fluid previously within the depression, thus importing and exporting material into and from the cavity (Yager et al. 1993).

The ecologic significance of depressions therefore becomes clear: Such pit formation can cause an increase in the sedimentation of particles, and especially of flocculent aggregates, with those changes probably resulting in the addition of nutrients. Furthermore, because of a reduction in the shearing stress, the amount and quality of food that is available to sessile deposit-feeder organisms is enhanced (Thiel et al. 1988). Another relevant effect involves an increasing larval recruitment (Thistle 1981; Thrush et al. 2003).

The review of Hall (1994) points out the existence of many species that cause this type of sediment disruption. Some examples are the stingrays (i.e., *Dasyatis sabina*; Thrush et al. 2006), the eagle ray (*Myliobatis tenuicaudatus*; Howard et al. 1977), flounder (*P. orbignianus*; Risk and Craig 1976), the gray whales (*Eschrichtius robustus*; Nelson et al. 1987), and Pacific walrus (*Odobenus rosmarus divergens*; Nelson et al. 1987; Thrush et al. 2006), although each one of these species produces a disturbance at a different order of magnitude (cf. also Daborn et al. 1993).

The present work was focussed on the feeding activity of the whitemouth croaker, *M. furnieri*, which is a major predator on tidal flats in the southwestern Atlantic (Sardiña and Lopez Cazorla 2005; Perillo et al. 2005; Valiñas et al. 2012). In these areas, a frequent observation regarding the activity of *M. furnieri* is the production of elliptical depressions in the mud resulting from the whitemouth croaker's feeding activity on the benthic infaunal organisms (Perillo et al. 2005; Fig. 2). *M. furnieri* is present on the American east coast from Veracruz, Mexico (20° 20' N) to El Rincón, Argentina (41° 00' S) and sporadically on the north coast of the San Matías Gulf (41° 10' S). This fish has also been sighted in the Caribbean islands (e.g., Cuba; Sardiña and Lopez Cazorla 2005).



**Fig. 1** Schematic representations of depression types. Shallow depression (a): the depth is equal to or less than the length in the direction of flow; deep depressions (b, c): the depth is greater than the length and below the sediment surface the eddy bifurcates vertically causing erosions of the walls of the depression from opposite directions. The points of separation and reattachment of the flow are illustrated by the lines in c. The solid arrows indicate the direction of flow, the thickness of the arrows indicates the relative rate of flow, and the wavy lines indicate the outer area of the slow stream.  $U_m$  flow,  $P$  primary vortex,  $S$  secondary vortex (Modified from Nowell and Jumars 1984)

Although such depressions have been shown to enhance sedimentation owing to a reduction in shear stress, certain studies have indicated that under specific flow conditions, those depressions tend to be filled with thinner sediment than the surrounding sediment (Risk and Craig 1976; Nelson et al. 1987). In the present investigation, the question arose as to what the effect was of the turbulence generated within the depressions on the resuspension of the sediment previously deposited therein—since those cavities are affected by the turbulent flow occurring in the salt marsh (Pratolongo et al. 2010)—and whether or not this resuspension would be selective with respect to different particle sizes.

The main hypothesis was that *M. furnieri* would promote a change in the granulometric composition of the sediment through the species's predatory activity, at the scale of a pit and at a broader landscape level (e.g. extrapolating effect based on density of pits). Thus, an increased particle coarseness was predicted that would decrease the critical bed-shearing stress and therefore reduce the stability of the sediment. The main aims of this investigation were to evaluate the effects of the feeding activity of *M. furnieri* on sediment stability and on the distribution of the infauna. Although many studies have focussed on the bioturbation activity of fish, that research has concentrated on effects on the recruitment and distribution of invertebrates, on the nutrient supply to deposit feeders, and on the migration of fauna (Thrush et al. 2003). This present report therefore constitutes one of the first attempts to determine the direct and indirect (mainly by affect the biota that live therein sediment) effects of a particular species of fish on the granulometric composition and stability of bottom sediment of salt marshes.

## Materials and Methods

### Study Area

The Bahía Blanca estuary is a large coastal wetland complex located on the southwestern Atlantic coast of Argentina, covering a total area of 2300 km<sup>2</sup> including about 410 km<sup>2</sup> of wetlands and more than 1150 km<sup>2</sup> of muddy tidal flats (Perillo et al. 2000). The tidal range is 2 m in the mouth and 3.8 m in the middle zones and headlands. Salinity increases from the mouth to the head where the restricted circulation and high evaporation can produce concentrations higher than 38 (Piccolo and Perillo 1990). The sampling area and where the experiments were performed was located in salt marshes close to Villa del Mar town (38° 52' 00" S 62° 07' 00" O, Argentina), characterized by the presence of a wide-marsh/salt-marsh cordgrass *Spartina alterniflora* located in the middle-lower intertidal zone (Pratolongo et al. 2010). At this place, a clear ecological zonation is observed along the intertidal fringe, with the lower limits of *S. alterniflora* marshes commonly



**Fig. 2** a Drawing of *Micropogonias furnieri*. The cause of the small depressions (pits) is shown in b. c A detail illustrating a representative pit. Lines indicating scale: 10 cm (a) and 1 cm (c)

occurring at the elevation of the mean high tide. Vegetated marsh takes place with extensive muddy patches without vegetation, and sediments from both areas are inhabited by a low diversity benthic infaunal community dominated by the polychaete *Laeonereis culveri* (Ieno and Bastida 1998; Molina 2013).

### Abundance and Activity of *M. furnieri*

Because the highest abundances of *M. furnieri* are usually recorded during the summer season (Valiñas et al. 2012), the samples ( $N = 28$ ) were taken in the summer of 2008 in vegetated and nonvegetated areas over the salt marshes during a high tide with a beach seine (length, 10 m; height 0.5 m; mesh size, 1 cm) which was hauled for 70 m parallel to the shore, being “shore” the marsh zone covered by the tide.

The abundance of individuals per hauls was compared between places, and the statistical significance of the data was analyzed by Kruskal-Wallis test, due to lack of normality (Zar 1999).

The distribution density of pits (the elliptical holes generated by action of *M. furnieri* when searching for food)—as a direct measure of the fish’s activity in vegetated and nonvegetated areas of salt marsh—was estimated by means of 1 m<sup>2</sup> plots ( $n = 24$  per site), during five consecutive days, but only fresh pits were recorded, as these can persist for about 1 day, depending on the climatic conditions. In addition, to determine if the size of the fish that were feeding at the two areas was different, the dimensions (length, width, and depth) of the pits were measured and the volume as a semiellipsoid was calculated, assuming that the volume of pits is a proportional measure of fish size (Johnson et al. 1983). The differences in pit abundance and size between areas were tested by the Student *t* test (Zar 1999). The percentage of the total area covered by pits was also estimated in each sample plot by multiplying the average area of the pits by their density. The same procedure was done to calculate the volume of sediment removed by bioturbation per area (Johnson and Nelson 1984).

### Characterization of the Sediment Within and Outside of the Depressions

Sediment samples from inside the pits and from the surrounding sediment were collected ( $n = 15$ ) to determine the particle size. The size distribution of sediment particles was obtained with a Malvern™ laser particle analyzer. The differences in the sediment-size distribution inside and outside the pits, expressed as the median grain size (D50 in  $\mu\text{m}$ ), were tested with a Kolmogorov-Smirnov test for two distributions (Sheskin 2004).

### Exclusion of *M. furnieri*

We investigated the effect of predation by *M. furnieri* on the erosion of the sediment. In its feeding, *M. furnieri* attacks the infaunal organisms (polychaetes, among other invertebrates; Martin 2002) living in the surficial layers of the sediment column. Biting the substrate produces an elliptical depression (i.e., the “pits.” around 2 cm depth), in which “negative spaces” (as the space between the surface of sediment and the bottom of the pit) could modify the transport and sediment deposition through changes generated on the flow over the muddy bed, as explained in the “Introduction” section. To evaluate if fish predation affected the abundance and vertical distribution of the preys along with the properties of the sediment, a fish-exclusion experiment was performed in the nonvegetated patches of salt marsh during the summer of 2008. Fish-exclusion barriers were placed along over bare patches (larger than 20 × 20 m) located in saltmarsh, because those areas were *M. furnieri*’s favorite feeding place (Valiñas et al. 2012). The experiment consisted of three treatments, since here called “zones” (six replicate each): (1) fish-exclusion (through the use of exclosures, four-walled cages), (2) control for cage effects (“semiexclosures” with two-walled cages, to mimic the effects of exclosures, but allowing fish to come inside), and (3) experiment control (areas delimited with labeled stakes). The 18 experimental units were clustered in six blocks established at similar elevations (1 block = 1 nonvegetated patch with a single replica of each treatment, separated 5 m each other in every single patch). Exclosures (4 m<sup>2</sup> in area and 1.5 m in height, to avoid that cage can go underwater) were constructed with 1-cm-mesh size plastic net. The lower borders of the mesh walls were buried 30 cm in the sediment. The upper borders contained buoys to keep the walls extended during high tide but enable them to drop down during low water. This exclosure design allowed predation by terrestrial organisms (e.g., shorebirds and crabs, personal observations) inside the cages during low tide so that any effect observed in these exclosures would be attributable specifically to fish predation (cf. Martinetto et al. 2005 for a similar design).

The experiment was conducted during the course of a month by collecting the sediment ends of samples obtained with a corer (10 cm in diameter and 12 cm deep, cut into three 4-cm layers of top, middle, and bottom) to measure the infaunal density with respect to depth. The samples obtained were sieved through a 0.5-mm mesh screen. In each sample, only polychaetes of the species *L. culveri* were isolated and counted. We evaluated only this species since those infauna were the exclusive benthic prey found in the gut contents of the fish (Valiñas et al. 2012). This could be due to the low diversity of polychaetes of similar size in the study area (Molina 2013), and also to taxonomical issues (*L. culveri* has prominent jaws that are easily observed under microscope; Valiñas et al.

2012). The differences between the depths and the densities measured in the three treatments were tested by a two-way analysis of variance (ANOVA; Zar 1999).

### *Sediment Stability*

Measurements of shearing stress and frictional speed, parameters that are related to sediment erodibility, were made from each zone. For this purpose, we used a cohesive-strength meter (CSM; Tolhurst et al. 1999), a portable device that measures the erosion thresholds of soft sediments. The CSM is a 30-mm-diameter cylinder that is partially buried in the sediment, and then filled with filtered sea water. A jet of water under pressure is applied to the sediment through a duct that opens into the cylinder. The velocity of the jet is systematically increased, and changes in turbidity from the suspension of sediment are recorded (as a percent decrease in transmittance) by means of a laser sensor placed inside of the cylinder. The device's small size enables observations of changes in stability down to a small spatial scale. The CSM's internal software then transforms these transmittance data into values of shearing stress and tangential velocities (for more details, cf. Tolhurst et al. 1999). Differences between the treatments were calculated by the one-way ANOVA (Zar 1999).

### *Concentrations of Chlorophyll *a* and Extracellular Polymeric Substances*

The first few millimeters of intertidal sediment contain a varied microbial and microphytobenthos biomass. Many of these organisms secrete carbohydrate-enriched extracellular polymeric substances (EPSs) to the surrounding matrix of the sediment which secretions may result in an increased interparticle cohesion and therefore an increased stability of the sediment (Underwood et al. 1995; Yallop et al. 2000). To determine the effect of fish predation on these substances, sediment samples were extracted to measure the EPS concentration (one sample per experimental unit), lyophilized, and the carbohydrates subsequently analyzed. Because the EPSs contain two different fractions of carbohydrates—the colloidal-S-extractable (i.e., solid-phase carbohydrate that is water soluble) and the ethylenediaminetetraacetic acid (EDTA)-extractable (i.e., carbohydrate that resists aqueous extraction in the absence of a chelating agent)—we proceeded as follows: for the colloidal-S-extracted, after the addition of 10 ml of distilled water to the lyophilized sediment, the samples were incubated for 1 h at 30 °C, then centrifuged for 5 min at 20,000×g. To remove the fraction of more firmly bound carbohydrates (the EDTA-extracted carbohydrate), the sediment was then extracted with 5 ml of a 100 mM Na<sub>2</sub>EDTA solution for 12 h at 20 °C and finally centrifuged for 5 min at 20,000×g (Underwood et al. 1995). The concentrations of colloidal-S- and EDTA-extracted carbohydrate were determined by the method of

phenol-H<sub>2</sub>SO<sub>4</sub> analysis, with glucose solution as a reference, an concentration curve plotted by measuring absorbance at 480 nm with a spectrophotometer, and a predictive function calculated (Dubois et al. 1956). A subsample of the lyophilized pellet was also used to determine chlorophyll *a* concentration by spectrophotometry (for details, cf. Lorenzen 1967). In all instances, differences among the results from the different zones were determined by the one-way ANOVA, and when differences were found, Tukey's test was performed (Zar 1999).

### *Sediment Grain Size*

We also determined the sediment grain size using a Malvern™ laser particle analyzer. Surficial sediment samples were extracted with a 3 × 0.5-cm (diameter × depth) minicorer. This sediment was analyzed without drying and a size-distribution curve of percentage per class vs. volume constructed. The differences in pellet-size distribution between the experimental zones with respect to the D<sub>50</sub> (μm) were analyzed with a nonparametric Kruskal-Wallis test for multiple groups (Sheskin 2004).

## Results

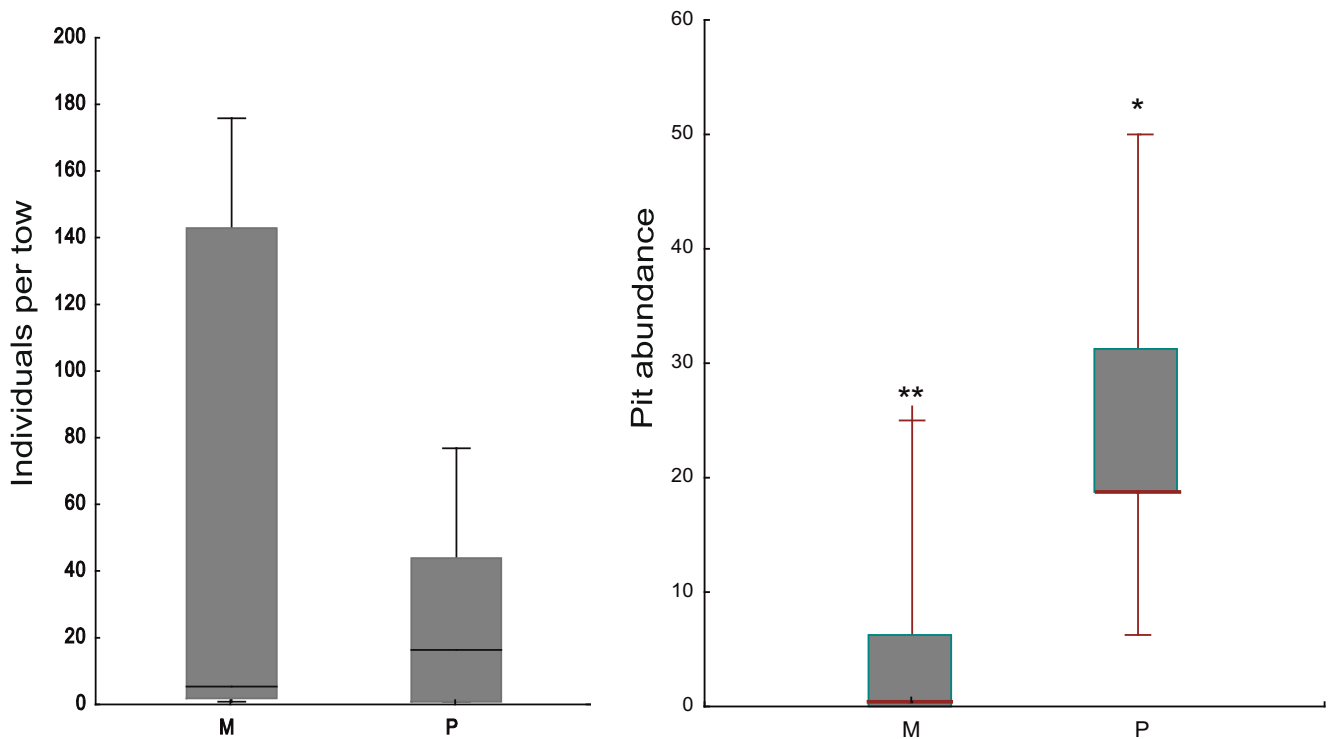
### *Abundance and Activity of *M. furnieri**

Given the lack of normality, the data were analyzed by the nonparametric Kruskal-Wallis test for two independent samples (Sheskin 2004). No differences were detected in the abundance of *M. furnieri* between the bare patches and the vegetated areas ( $p > 0.1$ ) (Fig. 3). The number of pits found was significantly higher in the nonvegetated environments ( $T_{[48]} = 7.38$ ;  $p < 0.001$ ; Fig. 3). Pit size, measured as the volume of individual pits, was also significantly higher in the nonvegetated areas ( $T_{[28]} = 5.12$ ;  $p < 0.001$ ), and the difference can therefore be attributed to the use of that space by larger individuals, being vegetation not an impediment to burning in the sediment, and with an identical feeding mode in both vegetated and nonvegetated places (Molina, personal observations).

The volume of sediment removed by bioturbation per unit of area was about 200 cm<sup>3</sup> m<sup>-2</sup> for the bare nonvegetated patches and 20 cm<sup>3</sup> m<sup>-2</sup> for the vegetated marsh (Fig. 4). The area occupied by pits was 18% in the former and 3.0% in the latter (Fig. 4).

### *Characterization of Sediment Inside and Outside the Depressions*

The results of the particle-size analysis indicated significant differences between the sediment from the interior of the



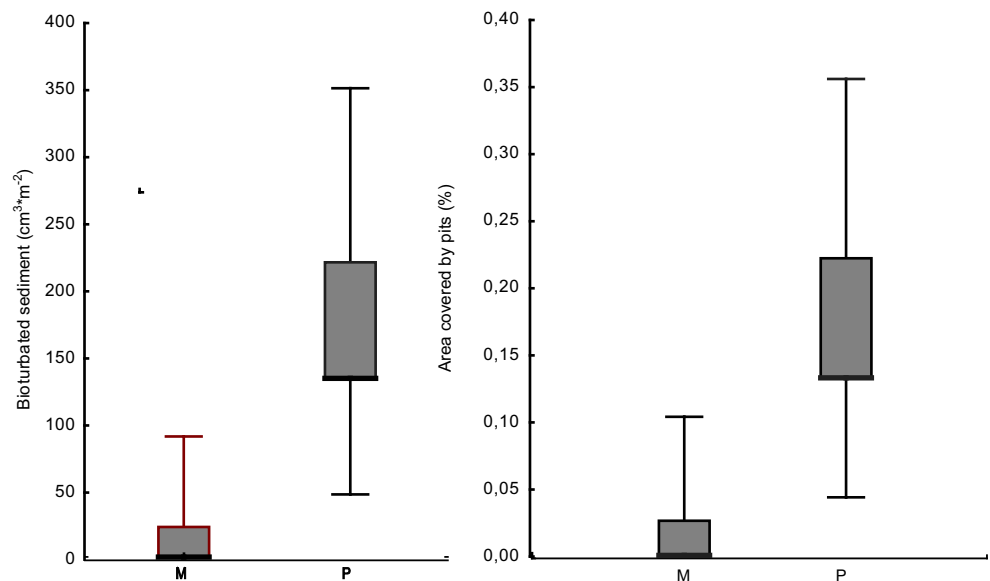
**Fig. 3** Abundance of *Micropogonias furnieri* throughout the study period of the summer 2007–2008. The abundance of *M. furnieri* in the vegetated (*M*) and nonvegetated (*P*) areas of the *Spartina alterniflora* marshes (*left panel*). In the figure, the number of *M. furnieri* individuals per netting is plotted on the *ordinate* for each of the two areas indicated on the *abscissa*. Abundance of *M. furnieri* pits in the marshes (*right panel*). In the figure, the number of pits per square meter is plotted on the *ordinate*

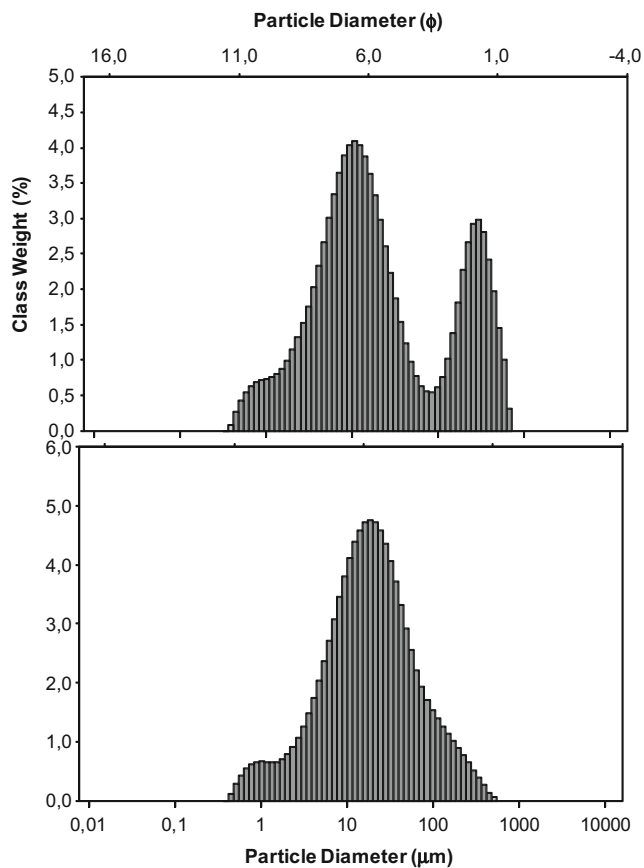
for each of the two areas indicated on the *abscissa*. Asterisks indicate statistically significant differences. In this and all subsequent figures, the graphic boxes were constructed with the upper and lower limits indicating the 25th and 75th percentiles, the *vertical lines* representing the 10th and 90th percentiles, and the *lines within the boxes* corresponding to the median of the data

depressions and the surrounding sediment (KS<sub>[16, 11]</sub>  $M = -0.938500$ ;  $p < 0.001$ ). The sediment from inside the pits

contained a high sand content, whereas in the surrounding sediment, sand content was lower (Fig. 5).

**Fig. 4** Volume of bioturbated sediment per 1 m<sup>2</sup> plot and percentage of area occupied by pits. In the figure, the volume of sediment bioturbated in cm<sup>3</sup> m<sup>-2</sup> is plotted on the *left* and the percent area covered by pits on the *right* for the nonvegetated areas (*P*) and the marshland (*M*) as indicated on the *abscissa*





**Fig. 5** Particle-size distribution inside (*upper panel*) and outside (*lower panel*) the pits in the sediment produced by the benthophagic fish *Micropogonias furnieri*. In the figure, the percent distribution of the particles having the sizes in micrometers indicated on the *abscissa* is plotted on the *ordinate* vs. those sizes on the *abscissa*

### Exclusion of *M. furnieri*

#### *Distribution of Infauna*

No significant differences were found in the abundance of *L. culveri* between the three experimental zones ( $F = 0.14$ ,  $df = 46$ ;  $p > 0.6$ ). No artifactual cage effects were observed that would have altered the measured variables since no statistical differences between zones 1 and 2 were found.

The distribution of *L. culveri* at the different strata of sediment depths was also not statistically different between the zones ( $p > 0.05$ ). In all three situations, a greater abundance of infaunal organisms was observed in the uppermost layer, with the density then decreasing downwards through the deeper layers (Tukey's  $T$  test  $p < 0.05$ ; Fig. 6).

#### *Sediment Stability*

Erosion analysis profiles obtained with the CSM indicated that in areas where predation by *M. furnieri* was allowed (i.e., in the experiment control, zone 3, and the control for cage

effects, zone 2), critical shearing forces were lower (with values ranging between 0.6 and 0.8  $\text{N m}^{-2}$ ,  $F = 45.0196$ ,  $df = 9$ ;  $p < 0.001$ ) than in the exclusion zone (with values greater than 2  $\text{N m}^{-2}$  by the Tukey's test,  $df = 9$ ;  $p < 0.001$ ), thus representing greater resistance to erosion (Fig. 7).

#### *Concentrations of Chlorophyll a and EPSs*

The chlorophyll *a* concentrations were significantly different between the experimental vs. control zones of the factorial experiment ( $F_{[2, 18]} = 25.3447$ ;  $p < 0.001$ ). The highest concentrations were found where the predatory activity of *M. furnieri* was disallowed (zone 1) and the lowest recorded in the experiment control area (zone 3) and the control area for cage effects (zone 2; Tukey's CM = 8.9752,  $df = 18$ ; Fig. 8).

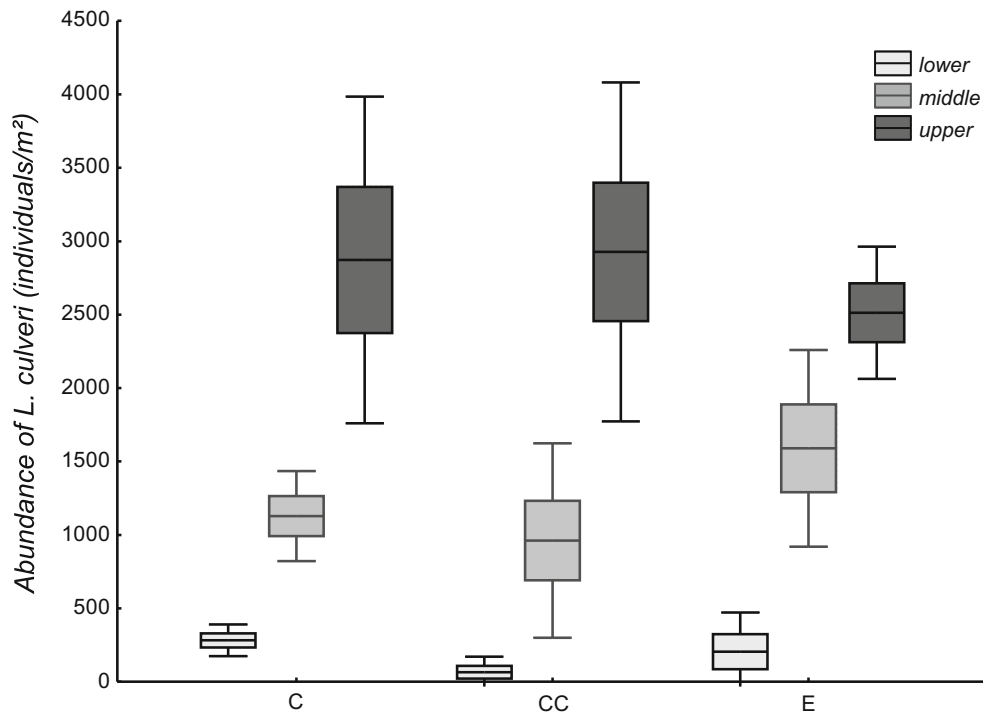
The concentrations of colloidal-S-extracted and EDTA-extracted EPSs exhibited a different behavior. The water-soluble fraction gave variable results, with no significant difference between the three zones ( $F_{[2, 12]} = 0.866$ ;  $p = 0.445$ ), whereas the EDTA-extracted EPS manifested a clear pattern in which statistically significant differences were found ( $F_{[2, 12]} = 4.08$ ;  $p < 0.05$ ). With those extracts, the *M. furnieri*-exclusion zone contained significantly higher concentrations than either of the two control zones (Tukey's CM = 28.6,  $df = 12$ ;  $p < 0.05$ ; Fig. 9).

#### *Sediment Grain Size*

Granulometric analysis of the sediment collected from the different zones indicated significant differences in the grain size (Kruskal-Wallis:  $H(2, 26) = 7.378196$ ;  $p = 0.0251$ ). The *M. furnieri*-exclusion zone had a finer sediment with lower amounts of sand than the sediments in the other two zones (multiple-comparisons  $z$  values, Kruskal-Wallis;  $p < 0.05$ ; Fig. 10).

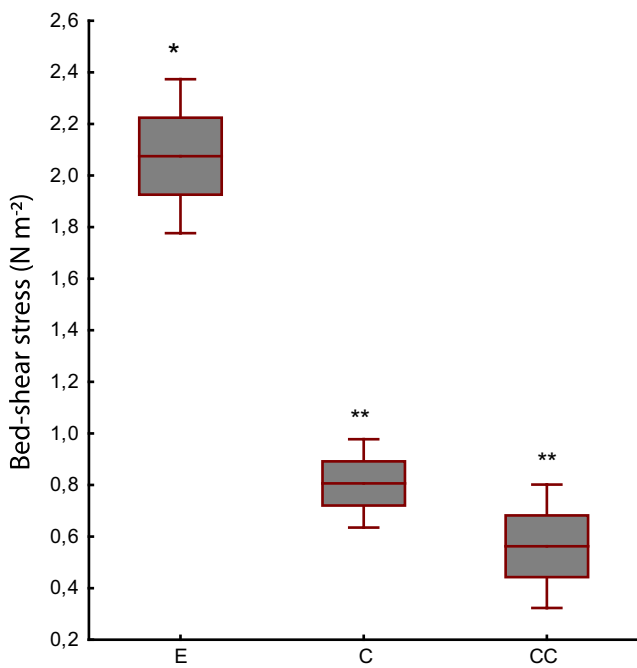
## Discussion

The analysis of *M. furnieri*'s influence on pit density in vegetated and nonvegetated habitats of salt marshes demonstrated that while the fish's density is not different in these environments, the eating habits were different (Figs. 3 and 4). The abundance and size of the pits (measured as the volume of an individual pit) generated by the croaker's foraging along with the amount of sediment that was removed from the substrate surface (measured as the aggregate volume of pits per unit of area) was greater at the nonvegetated sites. Sediment analysis from inside and outside the pits indicated that the grain inside the pits was larger than that found in the surrounding sediment. Such pits act basically as traps for coarse sediment where the fine sediment becomes washed away by subsequent turbulence. Although bottom sediments are characterized as

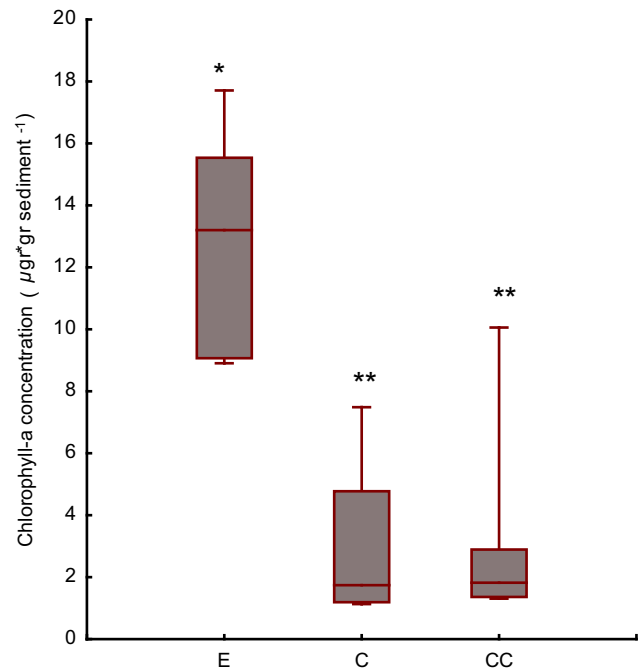


**Fig. 6** Density of *Laeonereis culveri* at different depths in the *Micropogonias furnieri*-exclusion experiment. In the figure, the abundance of *L. culveri* as individuals per square meter is plotted on the ordinate for each of the sediment depths indicated on the abscissa. White

boxes, lower depth; lighter-gray boxes, medium depth; darker-gray boxes, upper depth; C, experiment control (zone 3); CC, cage control (zone 2); E, *M. furnieri*-exclusion (zone 1)

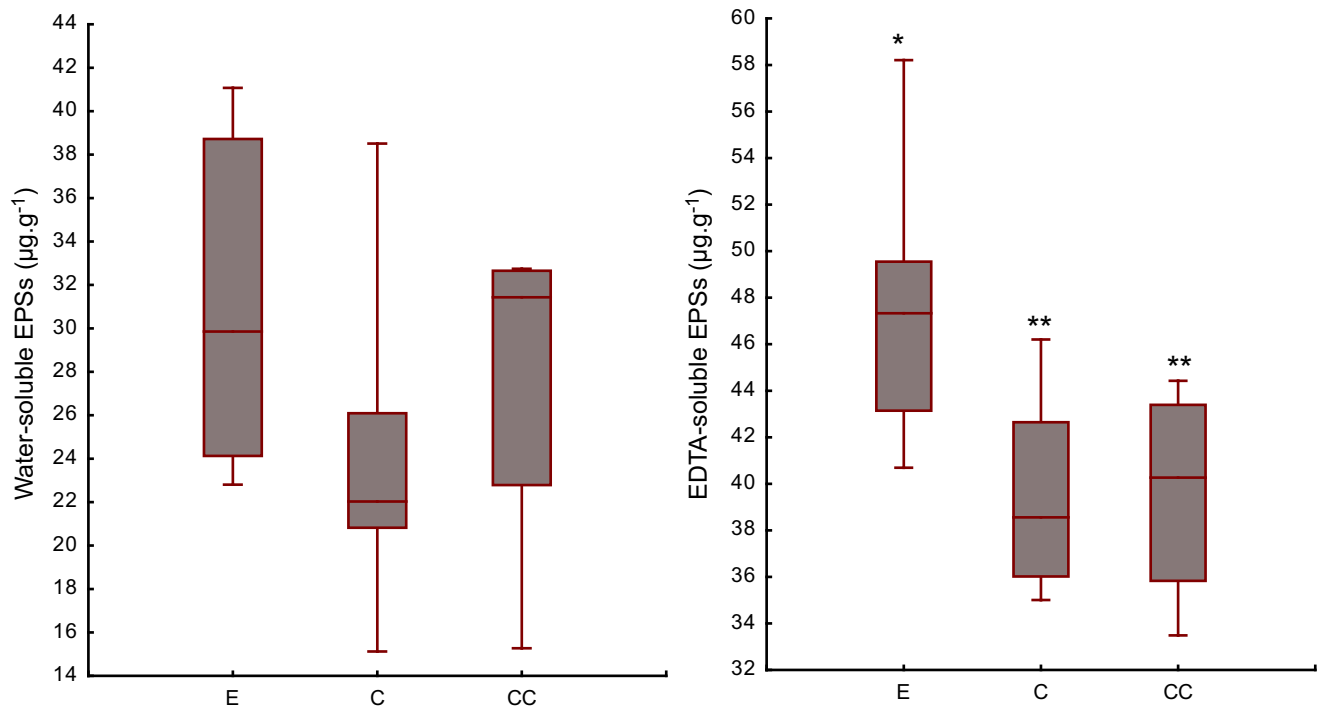


**Fig. 7** Average bed-shear stress for each zone in the *Micropogonias furnieri*-exclusion experiment. In the figure, the shearing force in Newton per square meter is plotted on the ordinate for each of the experimental zones indicated on the abscissa. E, *M. furnieri*-exclusion (zone 1); C, experiment control (zone 3); CC, cage control (zone 2). Single vs. double asterisks indicate a significant difference between the data ( $p < 0.01$ )



**Fig. 8** Chlorophyll *a* concentration in the different zones of the factorial experiment. In the figure, the chlorophyll *a* concentration in micrograms per gram of sediment is plotted on the ordinate for each of the experimental zones indicated on the abscissa. E, *M. furnieri*-exclusion (zone 1); C, experiment control (zone 3); CC, cage control (zone 2). Single vs. double asterisks indicate a significant difference between the data





**Fig. 9** Concentration of water-soluble EPSs and EDTA-soluble EPSs in the different zones of the factorial experiment. In the figure, the EPS extracted in micrograms is plotted on the *ordinates* for each of the

experimental zones indicated on the *abscissa*. *Left-hand panel*, water-soluble EPSs; *right-hand panel*, EDTA-soluble EPSs. *Single vs. double asterisks* indicate a significant difference between the data

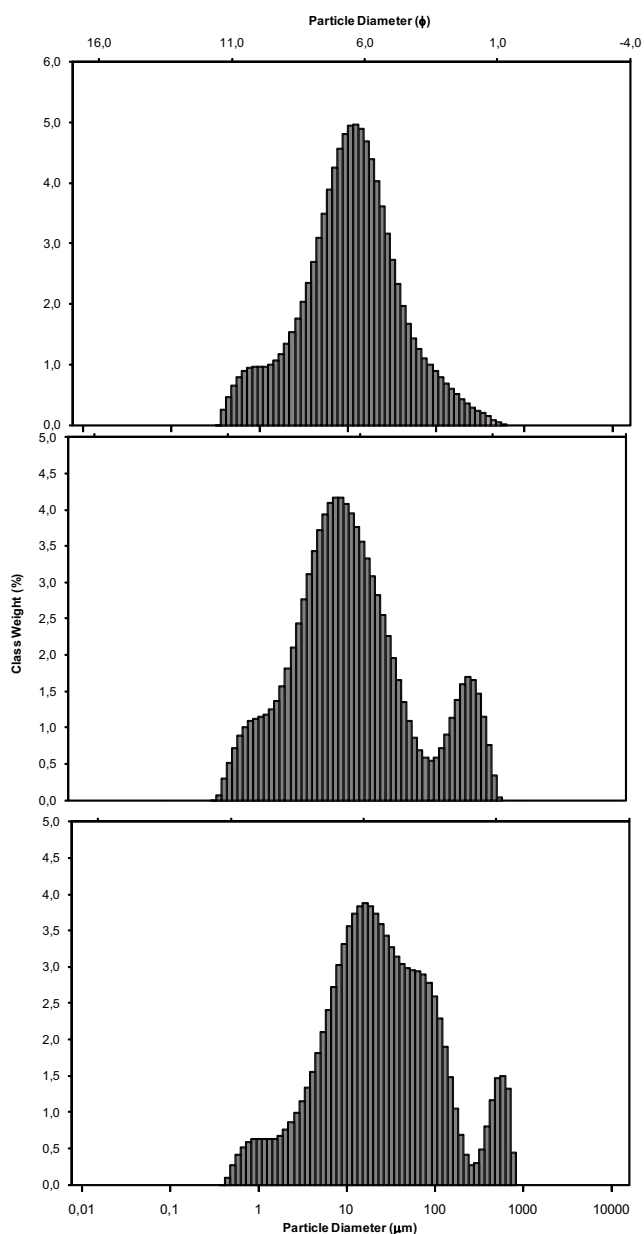
muddy, high amounts of sand transported as bedload were detected in previous studies at the sampling zone; however, it usually is deposited at high levels of the intertidal zone (Molina 2013)

Although no differences were found in the distribution of *M. furnieri* individuals between the vegetated and nonvegetated areas, this species showed a preference to areas without vegetation cover at the time of feeding since a greater abundance of pits was found in those environments. Although in previous investigations made by this research team (Molina 2013), a higher number of taxa were found in vegetated sites (mainly small species of polychaetes) living between the surficial roots of *S. alterniflora*, in contrast with nonvegetated sites, where we found a couple of big species of polychaetes (*L. culveri* and *Alitta succinea*), which could explain fish preference. Moreover, the volume analysis of the pits in the two areas indicated that the size of the fish that had foraged in the sediment was significantly greater in the nonvegetated areas (Fig. 3). Consistent with this interpretation is the observation that the amount of particles that were removed from bottom sediments by the activity of *M. furnieri* is greater in nonvegetated locations, in which quantity as measured in these experiments was around  $180 \text{ cm}^3 \text{ m}^{-2}$ . If these figures are extrapolated to the total area of nonvegetated places available to *M. furnieri* for foraging within the Bahía-Blanca estuary, the amount would be some  $20 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$ .

The pit-density data indicated that on the average the pits made by *M. furnieri* covered 18% of the nonvegetated places. Significance of the magnitude of pit coverage lies in the sediment composition within the pits—i.e., because of the foraging by *M. furnieri*, 18% of the nonvegetated areas is undergoing a change in granulometric composition. Since pit formation increases the sediment roughness, the critical erosion speeds become reduced (Cacchione and Drake 1982) and the composition of the infaunal communities could be altered (Thrush et al. 2003).

The quantitative effect of *M. furnieri* bioturbation is naturally much lower than that of large cartilaginous fish, such as rays (e.g., *D. sabina*), or of aquatic mammals, such as gray whales (*E. robustus*). A related and equally habitual species, such as the spot (*L. xanthurus*)—like *M. furnieri*, belonging to the family *Sciaenidae*—removes about 1% of the sediment surface (the upper 2 mm) per day, while feeding in South Carolina, USA (Billheimer and Coull 1988; Fleeger et al. 2006) Those results, being quantitatively lower than the values recorded in this study, would position *M. furnieri* as among the most impactful estuarine-fish bioturbators.

The exclusion experiment in this study was designed to determine if a bioturbating benthic fish modifies the abundance and distribution of benthic biota and the sediment stability, although our results indicated that the presence of the sciaenoid neither resulted in a decrease in benthic organisms



**Fig. 10** Sediment-particle-size distribution for the conditions of predator-exclusion, predation, and cage control. In the figure, the category of particle size, in micrometers, is plotted on the *ordinates* as a function of particle diameter on the *abscissas*. *Upper panel*, *M. furnieri*-exclusion with predation disallowed (zone 1); *middle panel*, experimental control with predation permitted (zone 3); *lower panel*, cage control with predation likewise permitted (zone 2)

in the nonvegetated areas nor affected the vertical distribution of the infauna. In contrast, when *M. furnieri* was excluded, the bottom sediment exhibited higher critical-shearing and frictional-velocity values than in areas where *M. furnieri* had access and therefore was less likely to be eroded, suggesting that through feeding, *M. furnieri* significantly modifies sediment stability.

Predator-exclusion experiments in marine soft-bottom habitats are frequent, which often do not demonstrate negative effects of predators on infaunal densities, and therefore demand a careful interpretation because failure to find differences between experimental sites may be attributable to several causes (Wilson 1991; Seitz et al. 2001). The exclusion of predators of the epibenthos not only does not cause infaunal predators to cease their activity, but the greater abundance of prey resulting from the absence of such predation competition may even constitute an advantage (Wilson 1991). Previous studies in this marshes have recorded high densities of such infaunal predators (Molina et al. 2009) as the marine worm *Priapulus caudatus*, Lamarck var. *tuberculato-spinosus* Baird; Stephen 1941, a large and very active species (Shirley 1990). The lack of differences between the experimental zones may therefore be owing to the presence of this predator. Although in the present experiments, the sampling was not designed to capture this type of organism, we, in fact, did record the presence of *P. caudatus* in the exclusions. Another justification to explain the lack of direct negative effects of *M. furnieri* could include the mobility of prey (i.e., moving out from exclusions) and an increase of intraspecific competition (densities could become lower because the negative effect of high prey densities), assuming that the original experimental designs were sufficiently powerful to detect predator effects (Thrush et al. 1994, and references therein).

We found no differences in the vertical distribution of the *L. culveri*, even though previous studies in the literature on the activity of predators similar to *M. furnieri* had detected differences in infaunal vertical distribution (Reise 1979; Fitzhugh and Fleeger 1985; Coull et al. 1989; Dittmann 1996). Those investigations focussed on the scale of the study to be analyzed and were concerned with measuring abundances at small intervals of depth (Coull et al. 1989; Quijón and Jaramillo 1996). In the present work, the densities were measured at depth intervals of 4 cm, which discrepancy in sampling could be one of the reasons why no differences were found in the results. Coull et al. (1989) proposed studying intervals of 1 or 2 mm for meiofauna and a maximum of 2 cm for macrofauna, because the authors considered that the effect of fish predation was evident only at the level of very small scales.

Predation may indirectly either stabilize or destabilize intertidal sediments. Indeed, the consumers of the microphytobenthos can alter the rate of erosion indirectly by preying on the stabilizers (here, the microphytobenthos; Daborn et al. 1993). In turn, predation by fish on the microphytobenthos-consumer organisms may produce a “cascade” effect by decreasing that prey density so as to enable the microphytobenthos to reach high densities, thus promoting sediment stability (Lei et al. 2010). In the experiments reported here, the concentrations of chlorophyll *a* as a direct measure of the abundance of microphytobenthos indicated the

opposite pattern to that expected since the highest concentrations were found in the absence of predators of the infaunal grazers. This result may have occurred because of an increase in the exclusion of those infaunal predators (i.e., *P. caudatus*) as well as the fish (Wilson 1991) coupled to the absence of the disturbances that the action of *M. furnieri* on the sediment surface generates (Thrush et al. 2003). This conclusion would imply that predation pressure by *M. furnieri* was also affecting, indirectly, the abundance of the microphytobenthos through the disturbance generated on the surface of the sediment and the consequent variation in grain size because the abundance of microalgae is always higher in cohesive rather than sandy sediments (Underwood and Paterson 1993).

The concentration of EPSs in sediments influences the threshold critical shearing stress for erosion (Dade et al. 1990; Underwood and Paterson 1993; Daborn et al. 1993; Lucas et al. 2003). Within the EPSs that are found in sediments—as mentioned in the “Introduction” section—two different fractions are present, the colloidal-S-extractable and EDTA-extractable EPSs (Decho 2000). From the standpoint of sediment stability, the colloidal-S-extractable EPSs have no known function: This fraction cannot be considered an inherent property of the sediment because incident light, water flow, or use by heterotrophic organisms will decrease the concentration of these EPSs (De Brouwer et al. 2000; Stal and De Brouwer 2003). This condition was reflected in the results of our factorial experiment with *M. furnieri*, where no significant trend or difference in this fraction was found in the sediments of the zones with and without predation. In contrast, the EDTA-extractable EPSs have a direct and constant effect on sediment stability (Paterson et al. 2000; De Brouwer et al. 2000), often being positively correlated with the concentration of chlorophyll *a* (Lundkvist et al. 2007). In our experiment, higher concentrations of EDTA-extractable EPSs and chlorophyll *a* were found in the fish-exclusion zone, possibly caused by an increase in the abundance of the microphytobenthos.

The stabilizing efficiency of this EPS fraction increases as the grain size decreases (Stal and De Brouwer 2003), thereby augmenting the sediment integrity, as was observed in the fish-exclusion zone. The average grain size was greater outside the exclusion zone or in places where the activity of *M. furnieri* disturbed the sediment surface. This change in particle size enhances the roughness of the bottom, thus increasing the Reynolds number while decreasing the critical shearing stress from erosion (Friend et al. 2005). The latter conclusion was verified in the present work by measurements made with the CSM (Fig. 7). Nevertheless, the sediment analysis results from the exclusion experiments that showed a coarser sediment composition in areas with fish activity than fish enclosures do not fit with the results from the characterization of the sediment within and outside of the depressions discussed above, which showed a coarser sediment inside pits than outside. These different results can be due to unintended

effects of cage itself and the distributions of them, beyond that there was no difference between cage controls and environment (Thrush 1991; Sewell 1996; Grafals-Soto and Nordstrom 2009). We have noted that one of side effects of cages could be the halting of sand bedload transport over sediment inside the cages.

The data from these experiments enabled us to conclude that the foraging action *M. furnieri* modified the stability of the sediment as a result of the predatory pressure the fish exerted on the organisms that inhabited vegetated and nonvegetated areas of salt marshes, resulting in the generation of elliptical depressions. That modification of the sediment stability was evidenced in two principal ways: (i) a negative effect on the microphytobenthic organisms that decreased the concentration of EPSs in the sediment and (ii) a consequent change in the roughness of the bottom and an alteration in the particle composition of the sediment where the fish had foraged.

This study increases our understanding of the role of biota in altering physical processes, especially our comprehension of the effects of epibenthic predators on biogeomorphological issues. The foraging pits made by predators are common in estuarine or coastal systems, and that fact suggests that other predators also influence the transport of sediment and the sediment stability in a direct or indirect way.

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