UNIVERSIDADE ESTADUAL PAULISTA “JÚLIO DE MESQUITA FILHO”

INSTITUTO DE BIOCIÊNCIAS DE BOTUCATU

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

ÁREA DE CONCENTRAÇÃO: ZOOLOGIA

DISSERTAÇÃO DE MESTRADO

O CONTEÚDO ORGÂNICO DO SEDIMENTO INFLUENCIA NA DISTRIBUIÇÃO INTRAESPECÍFICA DE CARANGUEJOS-CHAMA-MARÉ

FERNANDO R. DE GRANDE

Botucatu-SP

-2016-

FERNANDO R. DE GRANDE

O conteúdo orgânico do sedimento influencia na distribuição intraespecífica dos caranguejos-chama-maré

Dissertação apresentada ao curso de pós-graduação em Ciências Biológicas: Zoologia, do Instituto de Biociências, Universidade Estadual Paulista (UNESP), Campus de Botucatu, como parte dos requisitos para a obtenção do título de Mestre em Ciências Biológicas – Área de Concentração: Zoologia.

Orientadora: Dra. Tânia Marcia Costa

Botucatu-SP

-2016-

FICHA CATALOGRÁFICA ELABORADA PELA SEÇÃO TÉC. AQUIS. TRATAMENTO DA INFORM.
DIVISÃO TÉCNICA DE BIBLIOTECA E DOCUMENTAÇÃO - CÂMPUS DE BOTUCATU - UNESP
BIBLIOTECÁRIA RESPONSÁVEL: ROSEMEIRE APARECIDA VICENTE-CRB 8/5651

De Grande, Fernando Rafael.
O conteúdo orgânico do sedimento causa a distribuição intra-específica dos caranguejos-chama-maré / Fernando Rafael De Grande. - Botucatu, 2016

Dissertação (mestrado) - Universidade Estadual Paulista "Júlio de Mesquita Filho", Instituto de Biociências de Botucatu
Orientador: Tânia Marcia Costa
Capes: 20000006

1. Caranguejo - Distribuição geográfica. 2. Bentos. 3. Braquiuros. 4. Sedimentos.

Palavras-chave: Comportamento de preferencia; Delineamento experimental; Distribuição diferencial; Uca thayeri; Uca uruguayensis.

Dedico este trabalho a minha companheira Priscila Granado por ser a principal responsável para a concepção da ideia deste trabalho.

Agradecimentos

Esta dissertação é o resultado do trabalho de diversos envolvidos. Espero assim oferecer uma pequena demonstração de carinho e consideração aos que contribuíram para minha formação.

Agradeço a minha família por me incentivarem a continuar construindo minha carreira acadêmica. Agradeço aos meus pais, José D. De Grande e Sueli T. Comin De Grande, pelos anos dedicados a minha formação humana, por me proporcionarem uma educação de qualidade e por me fornecerem suporte financeiro. Agradeço ao meu irmão José Samuel de Grande e a sua esposa Andréia Marcon De Grande pelo carinho e orgulho demonstrado.

Agradeço aos amigos que integram a equipe do 'Laboratório de Ecologia e Comportamento Animal (Labecom)' – Unesp, Campus de São Vicente: Sanches F.H.C., Machado G., Oliveira R. Miyai C., Carvalho R., Jimenez P., Pardo J., Natálio L.F., Arvigo A., Citadin M., Cossignani E., Niero T., Ogata B., Fortuna M., Wendeborn M., Viana B., Fogo B.R. e Cordeiro L. por me ajudarem em tantas amostragens em campo, carregar sedimento, auxiliarem no delineamento, auxiliarem na estatística e darem sugestões sobre o trabalho. Agradeço-os por serem mais do que bons profissionais, por serem amigos.

Agradeço a Priscila Granado, minha companheira, que foi fundamental para a concepção da ideia deste trabalho. Agradeço-a pelo amor e atenção dedicado. Agradeço-a pelo companheirismo. Agradeço-a pelas discussões e pela motivação que tornam a carreira acadêmica uma carreira muito agradável.

Agradeço aos amigos da república mango Shultz L., Gonzalez J.G., Martins P.V., Alarcón J.A.F, Abib M.C., Souza V.A. e Stec A. por toda a amizade e companheirismo.

Agradeço ao professor Martin Skov (Bangor University) por me receber no País-de-Gales e pelas valiosas sugestões sobre o trabalho. Agradeço a professora Milene Fornari pelas sugestões para a realização da granulometria do sedimento.

Agradeço ao programa de pós-graduação em Ciências Biológicas (Zoologia) da Unesp de Botucatu e ao Campus do Litoral Paulistas da Unesp de São Vicente pela formação e estrutura física, respectivamente.

Finalmente agradeço a minha querida orientadora Tânia M. Costa, por toda a dedicação e zelo ao longo minha formação profissional.

Sumário

Apresentação

Os caranguejos-chama-maré (gênero *Uca*) são 'espécies-chave' dos ambientes estuarinos (Kristensen, 2008). Estes caranguejos promovem a bioturbação do sedimento durante suas atividades de alimentação e escavação de tocas (Kristensen, 2008). A bioturbação promovida por estes caranguejos altera a quantidade e a qualidade de recursos (matéria orgânica, oxigênio, microfitobentos) utilizados por outros organismos estuarinos (Botto and Iribarne, 2000; Kristensen, 2008; Michaels and Zieman, 2013). Além disso, os caranguejos-chama-maré são um dos organismos bentônicos mais abundantes na zona do entre-marés (Teal, 1962). Os hábitos anfíbios destes caranguejos os tornam importante presas tanto de organismos aquáticos quanto terrestres (Krumme et al. 2006; Koga et al. 2001). Desta forma estes caranguejos são um importante conector para o fluxo de energia e nutrientes proveniente da zona do entre-marés para ambientes adjacentes (Teal, 1962).

Uma característica interessante dos caranguejos-chama-maré é que diversas espécies podem coabitar a zona do entre-marés em faixas de ocupação relativamente distintas (Costa and Negreiros-Fransozo, 2001; Nobbs, 2003; Ribeiro et al. 2005). A distribuição diferencial também é notada a nível intraespecífico, havendo relatos de diferentes faixas de ocupação entre juvenis e adultos (Ens et al. 1993; Daleo et al. 2003). O estabelecimento das faixas de ocupação entre os caranguejos-chama-maré é determinado tanto por fatores abióticos quanto por fatores bióticos (Ribeiro et al. 2005; Sanford et al. 2006; Thurman et al. 2013; Mokhtari et al. 2015). Tais características tornam os caranguejos-chama-maré 'organismos-modelo' adequados para estudos sobre ecologia.

Dentre os fatores apontados como determinante para a distribuição diferencial entre os caranguejos-chama-maré, o conteúdo orgânico do sedimento é relatado como um dos principais. O conteúdo orgânico do sedimento é apontado como fonte de alimento para os caranguejos do gênero *Uca* (Crane, 1975; Icely and Jones, 1978, Reinsel and Rittschof, 1995). Um dos métodos mais usuais para se estimar a matéria orgânica do sedimento estuarino é o método de perda de peso por ignição (Luczak et al. 1997). Este método é capaz de detectar apenas a quantidade total de carbono do sedimento. No entanto estudos mais acurados vêm demonstrando que as espécies de chama-maré diferem quanto à qualidade do recurso alimentar ingerido (Hisieh et al. 2002). Cada espécie pode se alimentar de um recurso específico do sedimento (por exemplo: algumas espécies se alimentam mais de microalgas, outras de detritos vegetais, etc.). Isso nos conduziu a questionar se a matéria orgânica total do sedimento ainda é um fator que pode ser utilizado em estudos sobre ecologia dos caranguejos do gênero *Uca*.

Nós também observamos na literatura limitações lógicas sobre os delineamentos utilizados para estudar a influência da matéria orgânica do sedimento sobre a distribuição dos caranguejos-chama-maré. Tais limitações referem-se aos desenhos experimentais utilizados até então para a descrição do fenômeno e os seus respectivos limites intrínsecos. Neste trabalho nós tentamos superar tais limites propondo uma abordagem que buscou descrever o fenômeno no habitat dos chama-marés e o testou em experimentos em laboratório. Nossa última preocupação com este tema trata-se da conclusão comumente propagada de que os chama-maré 'preferem' sedimentos com mais matéria orgânica. Underwood et al. (2004) demostraram que comportamento de preferência não deve ser atribuído simplesmente a associações randômicas. Os autores propõem que estudos de preferência devem avaliar a utilização dos recursos envolvidos em tratamentos com e sem escolha.

Neste estudo nós avaliamos se o conteúdo orgânico do sedimento é um fator importante para a distribuição dos caranguejos-chama-maré e se, portanto, ainda pode ser utilizado em estudos sobre a ecologia desse gênero. Primariamente nós avaliamos em campo se a variação de tamanho e densidade de *U. thayeri* e *U. uruguayensis* está associada a variação de matéria orgânica do sedimento da zona do entre-marés. Em laboratório nós avaliamos a preferência de *U. uruguayensis* de diferentes tamanhos por sedimentos com alto ou baixo conteúdo orgânico. Complementarmente, avaliamos a quantidade de sedimento ingerido e número de tocas escavadas para cada tamanho de caranguejo em sedimentos com alto e baixo conteúdo orgânico.

Nós observamos para ambas as espécies que áreas com mais matéria orgânica suportam populações mais densas. Em laboratório observamos que independentemente do tamanho os caranguejos ingerem menos sedimento com alto conteúdo orgânico. Desta forma nós sugerimos que o conteúdo orgânico do sedimento indica a quantidade de alimento disponível para os chama-marés. Portanto este fator pode ainda ser utilizado nos estudos sobre a ecologia do gênero. Além disso, nós também observamos que os caranguejos apresentam uma associação negativa entre o tamanho corpóreo e o conteúdo orgânico. Em laboratório os indivíduos menores comem mais que os maiores, independentemente do tipo de sedimento. Devido a este último resultado, nós sugerimos que os caranguejos menores, que ainda estão crescendo, devem habitar sedimentos com maior quantidade de alimento. Conseqüentemente, em sedimentos com pouca matéria orgânica apenas caranguejos maiores, que gastam menos energia crescendo, podem sobreviver.

REFERENCIAS BIBLIOGRÁFICAS

Botto, F., Iribarne, O., 2000. Contrasting effects of two burrowing crabs (*Chasmagnathus granulate* and *Uca uruguayensis*) on sediment composition and transporting in estuarine environments. Estuar. Coast. Shelf S. 51, 141-151.

Costa, T.M., Negreiros-Fransozo M.L. (2001). Morphological adaptation of second maxilliped in semiterretrial of genus *Uca* leach, 1814 (Decapoda, Ocypodidae) from a subtropical Brazilian mangrove. Nauplius. 9, 123–131.

Crane, J., 1975. Fiddler Crabs of the World Ocypodidae: genus *Uca*, first ed. Princeton University Press, New York.

Daleo, P., Ribeiro, P., Iribarne, O., 2003. The SW Atlantic burrowing crab *Chasmagnathus granulatus* Dana affects the distribution and survival of the fiddler crab *Uca uruguayensis* Nobili. J. Exp. Mar. Biol. Ecol. 291:255–267.

Ens, B.J., Klaassen, N., Zwarts, L., 1993. Flocking and feeding in the fiddler crab (*Uca tangeri*): prey availability as risk-taking behavior. Neth. J. Sea Res. 31, 477–494.

Hsieh, H.L., Chen, C.P., Chen, Y.G., Yan, H.H., 2002. Diversity of benthic organic matter flows through polychaetes and crabs in a mangrove estuary: $\delta^{13}C$ and $\delta^{34}S$ signals. Mar. Ecol. Prog-Ser. 227, 145-155.

Icely, J.D., Jones, D.A., 1978. Factors affecting the distribution of the genus *Uca* (Crustacea: Ocypodidae) on an east African shore. Estuar. Coast. Mar. Sc. 6, 315-325.

Koga, T., Backwell, P.R.Y., Christy, J.H., Murai, M., Kasuya, E. 2001. Male-biased predation of fiddler crab. Anim. Behav. 62, 201-207.

Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. J. Sea Res. 59, 30-43.

Krumme, U., Keuthen, H., Saint-Paul, U., Villwock, W., 2007. Contribution to the feeding ecology of the banded puffer fish *Colomesus psittacus* (Tetraodontidae) in north Brazilian mangrove creeks. Braz. J. Biol. 67, 383–92

Luczak, C., Janquin, M., Kupka, A. 1997. Simple standard procedure for the routine determination of organic matter in marine sediment. Hydrobiologia. 345, 87-94.

Michaels, R.E., Zieman, J.C., 2013. Fiddler crabs (*Uca* spp) burrows have a little effect surrounding sediment oxygen concentration. J. Exp. Mar. Biol. Ecol.448, 104-113.

Mokhtari, M., Ghaffar, M.A., Usup, G., Cob, Z.C., 2015. Determination of key environmental factors responsible for distribution patterns of fiddler crabs in a tropical mangrove ecosystem. PloS one. 10, 01-17.

Nobbs, M., 2003. Effects of vegetation differ among three species of fiddler crabs (*Uca* spp.). J. Exp. Mar. Biol. Ecol. 284, 41–50.

Reinsel, K.A., Rittschof D., 1995. Environmental regulation of foraging in the sand fiddler crab *Uca pugilator* (Bosc 1802). J. Exp. Mar. Biol. Ecol. 187: 269-287.

Ribeiro, P.D., Iribarne, O.O., Daleo P., 2005. The relative importance of substratum characteristics and recruitment in determining the spatial distribution of the fiddler crab *Uca uruguayensis* Nobili. J. Exp. Mar. Biol. Ecol. 314:99–111.

Sanford, E., Holzman, S.B., Haney, R.A., Rand, D.M., Bertness, M.D., 2006. Larval tolerance, gene flow, and the northern geographic range limit of fiddler crabs. Ecology. 87, 2882–94

Teal, J.M., 1962. Energy flow in the salt marsh ecosystem of Georgia. Bull. Ecol. Soc. Am. 43, 614-624.

Thurman, C.L., Faria, S.C., McNamara, J.C. 2013. The distribution of fiddler crabs (*Uca*) along the coast of Brazil: implications for biogeography of the western Atlantic Ocean. Mar. Biodivers. Rec. 6, 01-21.

Underwood, A.J., Chapman, M.G., Crowe T.P. 2004. Identifying and understanding ecological preferences for habitat or prey. J. Exp. Mar. Biol. Ecol. 300, 161–187.

O trabalho a seguir será submetido à revista “Journal of Experimental Marine Biology and Ecology” e, portanto, está formatado conforme as normas disponíveis no website da revista: https://www.elsevier.com/journals/journal-of-experimental-marine-biology-and-ecology/0022-0981/guide-for-authors

SEDIMENT ORGANIC CONTENTS INFLUENCE THE INTRA-SPECIFIC DISTRIBUTION OF FIDDLER CRABS

Fernando Rafael De Grande[a] and Tânia Marcia Costa[b*]

[a]Postgraduate Program in Biological Sciences (Zoology), Botucatu Biosciences Institute, São Paulo State University – UNESP, 18618-000, SP, Brazil.

[b] Laboratory of Ecology and Animal Behavior. Coastal Campus, São Paulo StateUniversity – UNESP, 11330-900, São Vicente, SP, Brazil.

*Correspondingauthor: São Paulo State University – UNESP, Coastal Campus, Praça Infante Dom Henrique, S/N, Parque Bitarú. CEP: 11330-900, São Vicente, SP, Brasil. Tel: +55 13 3569 7116. E-mail address: costatm@clp.unesp.br (T.M. Costa).

Abstract

Crabs of the genus *Uca* are important benthic macrofauna in estuarine environments. Several *Uca* species coexist on intertidal mud- and sand-flats where they feed on microorganisms or sediment debris. Species have relatively distinct zones, and zone establishment is based on biotic and abiotic factors. Sediment organic matter is thought to be one of the most important zoning factors. We tested the effects of organic matter content on intra-specific distribution of *U*. *thayeri* and *U*. *uruguayensis* in their habitats. Organic matter content, crab density, and size frequency were observed in quadrates at each meter along intertidal transects (length of transect). In laboratory microcosms with- and without-options were used to test any preference of crabs for high- or low-organic content sediment. We also assessed feeding (scoops into sediment) and the number of burrows dug into each sediment for two categories of *U. uruguayensis* (large and small individuals). Both species showed a negative relationship between crab size and organic content, and both showed higher densities in field sites with more organic matter. This pattern was not due to a preference behavior of crabs for sediments that vary only by organic matter. Both sizes of crabs fed less frequently in sediments with high organic content. Small crabs feed more than large crabs regardless of the sediment type. Our results indicate that food organic matter influences the amount of food available to fiddler crabs. Because of this, sites with high organic content support populations at higher densities. In a mono specific patch, small crabs occupy the lower level of the intertidal zone, which contains more organic matter. Large crabs are predominant in the intertidal zone high level.

Keywords: preference behavior, experimental design, differential distribution.

1. Introduction

Fiddler crabs are of the most conspicuous benthic macrofauna in tropical and subtropical estuarine environments, both in abundance and biomass (Teal, 1962; Cammen et al. 1980; Macintosh et al. 2002; Koch and Wolff, 2002). Fiddler crabs are important to the trophic web of such environments because they alter the amount of resources available to other organisms in the intertidal zone (Kristensen, 2008). They affect the trophic web directly through consumption of resources when feeding and indirectly via bioturbation of sediment when digging burrows (Botto and Iribarne, 2000; Kristensen, 2008; Michaels and Zieman, 2013). Fiddler crabs are preyed upon by fish (Krumme et al. 2006), other crabs (Daleo et al. 2003), birds (Koga et al. 2001, 2015), and mammals (Rulison et al. 2012). They are therefore an important connector for the flow of energy and nutrients from the intertidal zone to aquatic and terrestrial environments (Teal, 1962). An understanding of the distribution of fiddler crabs is essential for the evaluation of their effects on other organisms and on the environment.

Fiddler crabs are useful models for evaluating the distribution, biogeography, and ecology of close competitors. Several *Uca* species typically coexist in intertidal areas where they share resources, including food and space. The distribution of fiddler crabs is regulated by macroscale factors, such as different latitudes (Crane, 1975, Sanford et al. 2006), and microscale factors, such as species zonation across the intertidal zone (Costa and Negreiros-Fransozo, 2001; Nobbs, 2003; Ribeiro et al. 2005). Important factors that govern the distribution of the fiddler crabs are abiotic factors like: the amount of organic matter, temperature, tide, salinity, and sediment grain size (Teal et al. 1958; Icely and Jones, 1978; Genoni, 1985; Reinsel and Rittschof, 1995; Ribeiro et al. 2005; Sanford et al. 2006; Thurman et al. 2013; Mokhtari et al. 2015), and biotic factors like: dispersion, larval settlement, predation, and sediment vegetation (Epifanio et al. 1988; Daleo et al. 2003; Nobbs, 2003; Thurman et al. 2013).

Sediment organic matter content is the source of food and is therefore an important factor for determining the distribution of fiddler crabs (Crane, 1975; Icely and Jones, 1978, Reinsel and Rittschof, 1995). Fiddler crabs have specialized maxillipeds for mechanical separation of organic particles from sediment grains (Miller, 1961; Costa and Negreiros-Fransozo, 2001; Colpo and Negreiros-Fransozo, 2013). In the intertidal zone, sediment organic matter has a gradient of distribution that decreases from water to land (Huettel et al. 1996; Lallier-verges et al, 1998; Bouillon et al. 2003). This gradient of organic matter is proposed to be the cause of coexisting *Uca* species zonation within an estuary (Icely and Jones, 1978; Kolch et al. 2005; Bezerra et al. 2006; Mokhtari et al. 2015).

Weight loss ignition is frequently used for quantifying the organic content and estimating the amount of total carbon in benthic environment sediment (Luczak et al. 1997), but this approach does not identify the source or quality of organic content. Accurate studies have shown that fiddler crab foods vary based on species, or on the area where they live (Hisieh et al. 2002). The main foods assimilated by *U. vocans* and *U*. *polita* consist of bacteria (Dye and Lasiak, 1987), while *U. vocator* feed on cyanobacteria (France,1998). *Uca arcuatacan* feed on diatoms and phanerogamic debris (Hsieh et al. 2002). Reinsel (2004) demonstrated that *U. pugilator* causes a reduction in organic content, chlorophyll A, and sediment meiofauna. Given the diversity of food items consumed by fiddler crabs, the amount of organic matter in the sediment may not reflect the actual food source. We investigated if total organic matter in sediment has any effect on crab distribution. One of our objectives was to determine if organic matter amounts can accurately be used in fiddler crab ecology studies.

We also aimed to address the logic that resulted from previous investigations into the effects of organic content on crab distribution. The main findings guiding this logic were based on: (1) the observation that different species of the genus *Uca* occupy the heights of the intertidal zone where variation in organic content occurs (Icely and Jones, 1978; Frith and Brunenmeister, 1980); (2) association tests between the population structure of one species and the amount of organic matter in the sediment (Costa and Negreiros-Fransozo, 2001; Ribeiro et al. 2005; Bezerra et al. 2006; Mokhtari et al. 2015); and (3) hypothesis tests to compare population structures across sites that differ in organic content (Colpo et al. 2003; Kock et al. 2005; Benetti et al. 2007). These three approaches have logical limitations (Underwood, 1997). First, it is impossible to know if species composition variation is promoted by organic content differences since this was not evaluated in the context of the population structure of each species. Secondly, the apparent association between population structure and organic content can be influenced by other factors. Finally, it is hard isolate the response variable (population structure) from other factors that may differ between sites including sediment grain size, tide level, predation, and other factors (Jennings and Nelson, 1992; Hughs et al. 1998; Daleo et al. 2003; Yang et al. 2008). Collectively, the effects of sediment organic content on the distribution of fiddler crabs remain unclear. Laboratory experiments (under controlled conditions) following the patterns observed in field could be used to test hypotheses built on each model.

Our final concern about the effects of organic content on species distribution related to the conclusion that fiddler crabs "*prefer*" sediments with higher organic content or food (Icely and Jones 1978; Ens et al. 1993; Thurman et al. 2013). Non-random associations are not equivalent to preference. The fact that animals are using more of one type of resources (e.g. food) than another, or that these resources are present in higher amounts in a certain microhabitat, are not necessarily indications of preference behavior (Underwood et al. 2004). '*Preference*' is when an animal actively chooses a resource from a group of resources that have the same chance of consumption, availability, and accessibility (Underwood et al. 2004). Complex experiments are required to assess the proportion of different types of items consumed, or habitats used by one animal, when those are offered singly and together in order to demonstrate preference behavior (see Olabarria et al. 2002 and Underwood et al. 2004).

We aimed to evaluate the effects of the amount of food organic matter in the intertidal zone sediment on intra-specific fiddler crab distribution. We evaluated if variation in organic matter content was associated with variation in the size, distribution, or density of fiddler crabs *U. thayeri* Rathbun, 1900 and *U. uruguayensis* Nobili, 1901. Two hypotheses were tested: (H_1) the density of fiddler crabs is higher in areas with more sediment organic matter, and (H_2) fiddler crabs are larger in areas with more sediment organic matter. We assumed that the effect of organic matter was strong enough to determine the variation in the distribution of crabs independently of other variables.

In the laboratory we used *U*. *uruguayensis* to test the hypothesis that (H3) both small and large fiddler crabs 'prefer' high organic content sediments. We also evaluated the use of sediments with either high or low organic content by crabs. We quantified how many scoops the crabs made while feeding and numbers of burrows they made in either high or low organic content sediments.

2. Methods

2.1 Field experiment: testing the relationship between fiddler crab size and density as a function of sediment organic content.

This study was conduct at two different estuaries in São Paulo State: the estuary at Mar Pequeno in Praia Grande, 23°59’S – 46°24’O and the estuary at Una River in Peruíbe, 24°26’S – 47°04’O. Both sites used for the study were mangrove forests under semi-diurnal tide systems.

Two species of fiddler crabs were evaluated: *U. thayeri* and *U. uruguayensis*. These species were selected because previous studies suggest that organic content is an important factor for their distribution (Costa and Negreiros-Fransozo, 2001; Bezerra et al. 2006; Ribeiro et al. 2005; Thurman et al. 2013).

Sediment organic content decreases when moving from water to land (Huettel et al. 1996; Lallier-verges et al. 1998; Bouillon et al. 2003). Fifteen transects perpendicular to the water line were made for each population between September 2014 and February 2015. A square was placed at each meter of the transect (75 cm side) where 5 sediment samples, each 5 mm in depth with a core of 3.2 mm diameter, were collected. We only collected the surface portion of the sediment because we assumed that the organic content of the sediment surface reflected the food accessed by crabs, regardless of quality. Samples of sediment were placed into labeled plastic bags and frozen. In the laboratory, samples were dried at 72 °C for 48 hours and incinerated at 550 °C for 5 hours (adapted from Luczak et al. 1997). The percentage of organic matter was obtained by subtracting the weight of the incinerated material from the weight of the dry sample. Each burrow inside all squares was excavated and all crabs were collected, identified, and measured (maximum carapace width in mm). The crabs were released into their habitat after measurements.

The criterion used to start or end transects was the presence or absence of the species of interest. This assured the evaluation of the effects of organic sediment contents only within the population boundaries.

2.1.1 Statistical analyses

Analysis of Co-Variance (ANCOVA) was used to compare the relationship of crab size or crab density to organic matter content between estuaries. Treatments represented the different estuaries for analytical purposes, and their covariate was the percentage of organic matter. First, we tested for differences between the slopes of the relationship between variable response and organic content in sediment at different estuaries. If slopes were homogeneous, it was valid to test for differences between size and density at estuaries after consideration of any relationship to sediment organic matter content. If slopes were not homogeneous, we used either a t-test to compare size and density between estuaries or linear regression to test any relationship between size, density, and percentage of organic content in each estuary. We evaluated the assumption of homogeneity in sample variances using Levine's test, and log (x + 1) transformed data when this assumption was violated.

2.2 Laboratory experiment: testing the intra-specific preference of fiddler crabs for different sediment organic contents.

2.2.1 Experimental design

We used *U. uruguayensis* males as a model organism to test the intra-specific preference of fiddler crabs for sediments with either high or low organic content. We selected this species because it demands little space and sediment because of its small size. We evaluated two crab sizes based on the mean ± standard error carapace width ($t = 21.92$, $df = 94$, $p < 0.001$): large crabs (11.89 ± 0.23 mm) and small crabs (8.07 ± 0.88 mm). *Uca uruguayensis* reaches sexual maturity at about 7 mm of carapace width (Hirose et al. 2013), but this size presented challenges for making observations. Thus, we chose to use larger, sexually mature crabs. Crabs were collected from the Praia Grande estuary (described in section 2.1), taken to the laboratory, and introduced to treatments conditions (described below in this section) on the same day.

To evaluate the selection of crabs based on differing organic content, we made microcosms (glass containers: 40 x 10 x 20 cm) divided into two compartments (20 x 10 x 20 cm) filled with a sediment column of 10 cm. The area of the microcosm was based on the maximum density of *U. uruguayensis* observed at the Praia Grande estuary (see in the results, section 3.1.1), so that each compartment was sufficient for enclosing the territory of an individual crab (around 14 cm^2). The depth of the sediment column (10cm) was established in accordance with the maximum depth of the burrow for this species (Machado et al.2013). We used one crab per microcosm to avoid intra-specific competition for territory as an interference factor.

We recorded the number of times each crab scooped the sediment and put it into his mouth, and the number of burrows in each compartment. The preference of large and small *U. uruguayensis* for sediments with differing organic content was tested using an experimental design (Figure 1, number of replicate per treatment = 12) based on the work of Olabarria et al. (2002) and Underwood et al. (2004). To avoid the initial selection of crabs for a specific side of the microcosm as an interference factor, half of the animals were released on the left side and the other half were released on the right side for each treatment. One side was systematically selected as reference (indicated by a subscript *t* in each treatment, Figure 1).

We compared the proportion of scoops and burrows dug in each sediment type with and without choice. The proportion of scoops or burrows was calculated for each treatment, and in both compartments, including the selected compartment.

Thus, the preference of *U. uruguayensis* for sediments with high organic content could be indicated by a greater proportion of scoops or burrows dug into this type of sediment, compared to what is expected by chance if no preference was expressed. The chance of crabs scooping the sediment and building burrows in each microcosm compartment was estimated from treatments where there was no choice. Preference for sediments with high organic content was assumed when the following hypothesis was accepted

$$H_3: \frac{n_{H_t1}}{N_1} > \frac{n_{H_t2}}{N_2}, \frac{n_{L_t3}}{N_3} > \frac{n_{L_t4}}{N_4}$$

In this equation, n_{H_ti} or n_{L_ti} is the number of scoops or burrows observed in each microcosm compartment (*High: H* or *Low: L* organic content) selected (identified by subscript *t*); *N* is the total number of scoops or burrows observed in both compartments; and i = 1,2,3 e 4 indicates the treatment. The selected treatment was 1 e 4, and without selection was 2 and 3 (figure 1).

If crabs prefer sediments with high organic content then the proportion of scoops, or burrows dug, in selected compartments (indicated by subscript *t*) for treatments 1, 2, and 3 must be greater than that observed for treatment L_t4. Consequently, in treatment 4, crabs tended to feed and build their burrows in the high organic matter compartment (H), supporting the use of L_t. In treatments with no choice (2 and 3) crabs had equal chances to feed and build burrows in either compartment. It is hypothesized that the proportion of scoops and burrows in H_t1 is larger than H_t2 e H_t3.

The preference of *U. uruguayensis* was evaluated for both large and small crabs, but not between size classes. The comparison of the total amount of scoops or burrows dug between the large and small crabs in each type of sediment was performed only between treatments.

2.2.2 Details about microcosm preparation

To obtain different organic contents we collected sediments from the upper level (lower organic content) and lower level (higher organic content) of the intertidal zone. Sediment was collected from the Praia Grande estuary, where variation in organic matter perpendicular to the water line was previously assessed (as described in section 2.1). The sediment was only collected from within the *U. uruguayensis* distribution. We collect approximately 100 L of each sediment type. Sediment was collected on the same day of the experiment and homogenized in 20 L boxes. From each box we removed three 60 g samples for granulometric analysis following the method of Suguio (1973). Samples were homogenized, a portion of the 60 g was treated with H_20_2, and the treated portion was dried in an oven at 60 ºC for two days. Samples were then weighed and subjected to elutriation. Samples were then dried again and reweighed to obtain the percentage of mud (silt and clay). A set of sieves, with mesh sizes of 0.5 mm (very coarse sand), 0.25 mm (coarse sand), 0.125 mm (medium sand), 0.062 mm (fine sand), and 0.062 mm (very fine sand) were used to categorize sand types. Mechanical agitation was applied for 15 min with a sieve shaker and the frequency of each grade was expressed as percentage of total weight.

We put approximately 2 L of sediment in each compartment. Excess water was removed from the microcosm sediment surface with a sponge. We wait 24 hr to insert the crabs into the microcosms in order to stabilize the sediment biota. Before inserting the crabs, we collected 3 samples (about 10 g) from the sediment surface (approximately 0.5 mm deep) of each compartment with a small spoon. Samples were used to obtain the organic content by weight loss ignition (described in section 2.1).

We collected sediment from within the *U*. *uruguayensis* distribution. However, since we used sediments from different regions of the intertidal zone our methodology introduced a bias. Variables in the sediment besides organic matter are found perpendicular to the waterline, such as: grain size (Yang et al. 2009), humidity (Hughes et al. 1998), and biota (Jennings and Nelson, 1992). We previously tested other methods that use the same type of sediment (either artificial material or crab habitat sediment) and we varied the organic content using ration (method used by Rodríguez et al. 1992) or humus. These methods were not effective for *U. uruguayensis* because they did not feed and some died. The interest of our work is focused on the effects of organic matter on fiddler crab populations, and we assume that organic content is inseparable from other sediment variables.

Crabs remained in treatments to acclimate for a time period that was established based on preliminary observations where we evaluated the number of active animals in the sediment surface. After 120 hr of acclimation each crab was observed for 10 min and the number of scoops and burrows were recorded. All animals were observed on the same day. Animals were kept on a light regime consisting of 12 hr of light and 12 hr of darkness, and at an average temperature of 30.0 °C (SD ± 1.0). Microcosm walls were covered with opaque, black plastic to avoid visual interference between animals.

This research had permission from the system of authorization and information on biodiversity (Sisbio) of the Brazilian Ministry of the Environment (number: 47478-1).

2.2.3 Statistical analyses

Hypotheses on crab preferences were evaluated using one-way analysis of variance (ANOVA). Comparisons between the number of scoops and burrows dug by large and small crabs in each type of sediment were carried out using a two-way ANOVA. Similarly, a two-way ANOVA was used to assess the percentage of organic matter in sediment microcosms used for large and small crabs. In all cases we evaluated the assumption of homogeneity and variance of samples. We considered 95% as a significance level. In instances of significant difference we used the post-hoc Scheffe test.

3. Results

3.1 Field experiment

3.1.1 Density variation of fiddler crabs

At the *U. thayeri* site of Praia Grande the variation in the percentage of sediment organic matter was larger (0.06 to 23:43, mean 8.99%) than that observed at Peruíbe (1.66 to 11.90, mean 5.91%). The population density of *U. thayeri* was higher at Praia Grande (2.04 to 34.0, mean 8.73 individuals per m²) compared to Peruíbe (2.0 to 24, mean 4.43 individuals per m²; $t = 3.09$, df = 297, $p = 0.002$). The relationship between organic content densities differed between estuaries for *U. thayeri* (Figure 2 A and B; $F_{1,295} = 5.97$, $p = 0.04$, ANCOVA). There was a significant negative relationship between the density of *U. thayeri* and organic content at Praia Grande (Regression analysis: $F_{1,179} = 28.22$, $r^2 = 0.136$, $p < 0.001$), but there was no such relationship at Peruíbe ($F_{1,116} = 0.22$, $r^2 = 0.002$, $p = 0.635$).

At the Praia Grande *U.uruguayensis* site variation in organic content was greater (0.01 to 9.55, mean 1.7 %) than it was at Peruíbe (0.48 to 6.18, mean 2.27 %). There was no difference between estuaries in the relationship of crab density to sediment organic matter (Figure 2 C; ANCOVA, interaction term *Location*Organics*: $F_{1,225} = 1.118$, $p = 0.291$). At Praia Grande, *U. uruguayensis* density was lower (2.04 to 59.18, mean 14.72 individuals per m²) than at Peruíbe (4.08 to 177.55, mean 38.77 individuals per m²; $F_{1,226} = 57.978$, $p < 0.0001$, ANCOVA). The effect of organic matter on the density of these crabs also differed between the two populations ($F_{1,226} = 541$, $p = 0.021$, ANCOVA). Linear regression did not show a relationship between the density of *U. uruguayensis* and the organic matter content at Praia Grande ($F_{1,91}$= 8.335, r^2 = 0.08, p = 0.05) or at Peruíbe ($F_{1,134}$ = 0.290, r^2 = 0.02, p = 0.591).

3.1.2 Size variation of fiddler crabs

In both estuaries the size of *U. thayeri* decreased with organic matter increase. There was no difference between estuaries in crab size to sediment organic matter relationship (ANCOVA, interaction term *Location*Organics*: $F_{1,295}$= 0.008, p = 0.930). Average crab size differed between estuaries ($F_{1,296}$= 16.010, p < 0.001). At Praia Grande *U. thayeri* crabs were smaller (3.3 to 22.8, mean 9.9 mm) than they were at Peruíbe (3.6 to 24.3, mean 12.6 mm). Data from the two estuaries were therefore pooled. A linear regression on these pooled data found a negative relationship between the size of *U. thayeri* and sediment organic matter content (Figure 3 A; $F_{1,297}$= 4.47, r^2 = 0.015, p = 0.035).

In both populations the size of *U. uruguayensis* decreased as organic matter increased. There was no difference between estuaries in the crab size to sediment organic matter relationship (Figure 3 B; ANCOVA, interaction term *Location*Organics*: $F_{1,225}$ = 0.121, p = 0.728). At Praia Grande, *U. uruguayensis* crabs were larger (0.9 to 10.72, mean 6.4 mm) than at Peruíbe (3.4 to 7.6, mean 5.4 mm; $F_{1,226}$ = 0.058, p = 0.025, ANCOVA). The effects of organic matter on the size of *U. uruguayensis* differed between estuaries ($F_{1,226}$ = 11.026, p = 0.01). At Praia Grande the relationship of organic content to crab size was smaller ($F_{1,91}$= 5.56, r^2 = 0.058, p = 0.02) than at Peruíbe ($F_{1,134}$= 11.28, r^2 = 0.078, p = 0.001).

3.2 Laboratory experiment

3.2.1 Organic matter and grain size of microcosm sediment

The mean ± standard error of the organic content of sediments used in microcosms was 5.84% ± 0.19 and 1.81 ± 0.12% for groups with high and low organic matter, respectively. The difference in organic matter was observed between microcosm compartments, depending on the treatment used (ANOVA, interaction term *tratament*compartment*: $F_{3,176}$ = 66.155, MS = 134.026, p < 0.0001). In treatments with no choice, organic matter did not vary between compartments (p < 0.05, Scheffe test). In multi-choice treatments, organic matter in sediment was greater in one compartment relative to another (p < 0.001, Scheffe test).

Both sediment types were primarily composed of mud, sand, and fine sand. High organic content sediment was composed of: 34.10 % mud, 1.55 % very coarse sand, 1.11 % coarse sand, 1.43 % medium sand, 24.59 % fine sand, and 36.40 % very fine sand. Low organic content sediment was composed of: 45.07 % mud, 0.23 % very coarse sand, 1.22 % coarse sand, 2.75 % medium sand, 23.26 % fine sand, and 26.40 % very fine sand.

3.2.2 Organic matter and habitat preference

Uca uruguayensis has no preference for feeding or habitat areas based on sediment organic matter (figure 4 A and B). The proportion of scoops was essentially the same between treatments for large crabs (one-way ANOVA: $F_{3,44} = 0.7612$, MS = 0.1624, $p = 0.5219$) and small crabs (one-way ANOVA: $F_{3,44} = 0.2382$, MS = 0.0571, $p < 0.8692$). Moreover, *U. uruguayensis* did not show a burrowing location preference. The proportion of burrows did not differ between treatments for either large crabs (one-way ANOVA: $F_{3,44} = 0.6564$, MS = 0.0461, $p = 0.5832$) or small crabs (one-way ANOVA: $F_{3,44} = 1.7544$, MS = 0.1471, $p < 0.1698$).

3.2.2 Comparison of sediment ingesting and burrows dug by different size crabs in different sediment types

The amount of sediment ingested by crabs differs between treatments (two-way ANOVA: $F_{1,44} = 22.6110$, MS = 203580.8, $p < 0.0001$) and sizes (two-way ANOVA: $F_{1,44} = 13.6856$, MS = 123221.3, $p = 0.0005$). Crabs of both sizes fed more frequently in low organic content microcosms (mean ± SD of scoops in the sediment = 152.16 ± 5.16) compared to those with high content (figure 5, A; mean ± SD = 78.02 scoops in the sediment ± 3.46). Large crabs scooped the sediment 67.04 (SD± 3.19) times and small crabs scooped 173.5 (SD± 5.82) times, regardless of treatment (Figure 5, A). Crabs dug approximately one burrow per compartment (mean± SD: 0.92 ± 0.12), regardless of size (two-way ANOVA: $F_{1,44} = 0.4658$, MS = 1.0208, $p = 0.4984$) or amount of sediment organic matter (figure 5, B; two-way ANOVA: $F_{1,44} = 0.0095$, MS = 0.0208, $p = 0.9227$).

4. Discussion

Organic content variation in intertidal surface sediments promotes intra-specific differential distribution of fiddler crabs. Sites with higher organic content support higher density populations. Within a mono-specific patch, larger crabs predominantly inhabit the upper level of the intertidal zone where less organic matter is present. Distribution patterns are not the result of crab preference behavior by the amount of organic matter in the sediment. Crabs spend less time feeding on sediments with more organic matter. We suggest that the organic matter levels in the sediment surface indicate the amount of available food for crabs, regardless of the specific food item by a species. Because of this, sites with more organic matter support higher density populations. We observed that large crabs feed less frequently than smaller crabs and we propose that large crabs can survive in the upper intertidal zone where less organic matter is present.

Fiddler crabs eat bacteria, micro-algae, plants, debris, or meiofauna from the sediment surface (Haines and Montague, 1979; Dye and Lasiak, 1987; Currin, 1995; France, 1998; Hisieh et al. 2002; Reinsel, 2004). Regardless of the quality of the food, this study demonstrates that amount of the total organic matter in the sediment surface has an effect on crab distribution. We observed that both *U. thayeri* and *U. urugayensis* populations are at higher densities at sites where the sediment contains more organic matter. The relationship that we observed between crab size and sediment organic matter content was weak. We assert that associations are not enough to explain the effects of one variable on another because any third variable could be the cause of the apparent association between the first two (Underwood, 1997; Zar, 2010). However, the relationship between the density of *U. thayeri* and *U. uruguayensis* and sediment organic content is consistent with previous findings (Costa and Negreiros-Fransozo, 2001; Ribeiro et al. 2005; Bezerra et al. 2006). Despite the limits of this logical approach, our laboratory experiment results clearly show that crab feeding depends on the amount of organic matter in the sediment and size of the animal. *Uca uruguayensis* individuals eat less in sediments with higher organic content. Based on our findings, the hypothesis that sediment organic content influences the distribution of the fiddler crabs is valid. The quantitative method of ignition weight loss is a useful tool in studies on fiddler crab distribution.

Other studies show that fiddler crab density is associated with sediment organic matter (Costa and Negreiros-Fransozo, 2001; Bezerra et al. 2006; Ribeiro et al. 2005; Mokhtari et al. 2015). Organic matter is a source of inter-specific zonation of fiddler crabs (Kolck et al. 2005;

Bezerra et al 2006; Mokhtari et al. 2015). It is suggested that *U. thayeri* and *U. chlorophthalmus* prefer to inhabit mangrove forests or lower regions of the intertidal zone because sediment organic content is greater in these locations, thus resulting in higher densities of these species relative to other species (Icely and Jones, 1978; Thurman et al. 2013). While *U. uruguayensis* are at higher densities at sites with high organic matter, in controlled laboratory tests we found that this species does not select feeding areas based on the parameters we tested. Therefore, inter-specific zonation should not be attributed to the preference of crabs for different types of sediment alone. Moreover, in three of the four populations studied density was not associated with variation in organic matter perpendicular to the waterline. Based in this we suggest that organic matter is not the only factor influencing fiddler crab species zonation.

Other factors can influence the range occupied by each fiddler crabs species. For example, species differ in the morphology of their maxillipeds (Costa andNegreiros-Fransozo, 2001; Colpo and Negreiros-Fransozo, 2013). This can influence species zonation based on the distribution of sediment grain size in the intertidal zone (Costa and Negreiros-Fransozo, 2001, Mokhtari et al 2015). Furthermore, different species of crabs are known to consume different food items (Hisieh et al. 2002). The differential availability of food items could define different occupancy bands between species (Hisieh et al. 2002; Weis and Weis, 2004). Fiddler crabs also have different tolerances for salinity (Miller and Maurer, 1973) and dehydration (Herreid II, 1969). Such physiological differences may also influence crab occupation band. Based on our findings, sediment organic content influences only the distribution of each species.

At the intra-specific level, organic matter exhibits two effects on fiddler crab distribution. First, it affects the population density at different sites, with high organic content supporting a greater number of individuals. Higher density populations due to food amounts have been reported for blue crabs *Callinectes sapidus* (Seitz et al. 2003), island lizards *Podarcis gaigeae* (Parfilis et al. 2009), and red squirrels *Sciurus vulgaris* (Wauters et al. 2001). A greater abundance of food implies higher survival rates and a greater fitness of individuals (Cruz-Rivera and Hay, 2000). Ultimately, areas with more food maintain more individuals than areas with less food.

Second, organic content affects the distribution of different size crabs within the same patch. Again, preference cannot be attributed to the differential distribution observed between the large and small crabs. Large *U. thayeri* and *U. uruguayensis* individuals tend to inhabit the intertidal zone upper levels within a respective patch. This trend is also observed for *U. vocans* (Murai et al. 1983), *U. pugnax* (Bertness and Miller, 1984), and *U. tangeri* (Ens et al.1993). Ens et al. (1993) suggest that large fiddler crabs build burrows in the high level of the intertidal zone because of risk of predation by fish and blue crabs at low levels. Sediment hardness and the presence of plant roots are other factors that hinder burrow digging and may influence the differential distribution of crabs (Bertness and Miller, 1984). Under controlled, laboratory conditions, without the interference of other factors such as predators or roots, *U. uruguayensis* showed no preference for digging burrows in sediments that vary simply by organic matter.

However, small crabs fed twice as frequently as larger crabs in our tests irrespective of the sediment organic content. Among crustaceans, young individuals are known to feed more frequently than older individuals because of energy spent molting during growth (Hartnoll, 2001; McWillian and Phillips, 2007; Willian and Hartnoll, 2007). We suggest that the low level of the intertidal zone favor the survival of juvenile fiddler crabs because they require more food as they grow. Large fiddler crabs can survive in the upper regions of the intertidal zone where they also avoid predators. Future studies focusing on competition for space and qualitative aspects of the food eaten between juveniles and adults will expand the body of knowledge on the intraspecific distribution of fiddler crabs.

5. Acknowledgements

We thank Oliveira R., Miyai C., Carvalho R., Jimenez P., Pardo J., Natálio L.F., Arvigo A., Citadin M., Cossignani E., Niero T., Ogata B., Fortuna M., Wendeborn M., Vianna B., Fogo B., and Cordeiro L. for their help in field and laboratory work; Granado P., Sanches F.H.C. and Machado G. for suggestions in statistical analyses; and Fornari M. for her suggestion on particle size analysis. This work was financial supporting by grant #2014/00456-7, São Paulo Research Foundation (FAPESP) (De Grande, FR) and by the Brazilian Research Council (CNPq # 303400/2012-9) (Costa, TM).

6. References

Benetti, A.S., Negreiros-Fransozo, M.L., Costa, T.M., 2007. Population and reproductive biology of the crab *Uca burgersi* (Crustacea: Ocypodidae) in three subtropical mangrove forests. Rev. Biol. Trop. 55, 55-70.

Bertness, M.D., Miller, T., 1984. The distribution and dynamics of *Uca pugnax* (Smith) burrows in a New England salt marsh. J. Exp. Mar. Biol. Ecol. 76, 159-164.

Bezerra, L.E.A., Dias, C.B., Santana, G.X., Matthews-cascon, H., 2006. Spatial distribution of fiddler crabs (genus *Uca*) in a tropical mangrove of northeast Brazil. Sci. Mar. 70, 759–766.

Botto, F., Iribarne, O., 2000. Contrasting effects of two burrowing crabs (*Chasmagnathus granulate* and *Uca uruguayensis*) on sediment composition and transporting in estuarine environments. Estuar. Coast. Shelf S. 51, 141-151.

Bouillon, S., Rao, A.V.V.S., Koedam, N., Dehairs, F. 2003. Sources of organic carbon in mangrove sediments : variability and possible ecological implications. Hydrobiologia. 495, 33–39.

Cammen, L.M., Seneca, E.D., Stroud, L.M.,1980. Energy flow through the fiddler crabs *Uca pugnax* and *U. mina*x and the marsh periwinkle *Littorina irrorata* in a North Carolina salt marsh.Am. Midl. Nat. 103, 238-250.

Colpo, K.D., Negreiros-Fransozo, M.L., 2003. Reproductive output of *Uca vocator* (Herbst, 1804) (Brachyura, Ocypodidae) from three subtropical mangroves in Brazil. Crustaceana. 76, 1-11.

Colpo, K.D., Negreiros-Fransozo, M.L., 2013. Morphological diversity of setae on the second maxilliped of fiddler crabs (Decapoda: Ocypodidae) from the southwestern Atlantic coast. Invertebr. Biol. 132, 38-45.

Costa, T.M., Negreiros-Fransozo M.L. (2001). Morphological adaptation of second maxilliped in semiterretrial of genus *Uca* Leach, 1814 (Decapoda, Ocypodidae) from a subtropical Brazilian mangrove. Nauplius. 9, 123–131.

Crane, J., 1975. Fiddler Crabs of the World Ocypodidae: genus *Uca*, first ed. Princeton University Press, New York.

Cruz-Rivera, E., Hay, M., 2000. Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine meso grazers. Ecology. 1, 201-219.

Currin, C.A., Newell, S.Y., Paerl, H.W., 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. Mar. Ecol-Prog. Ser. 121, 99–116.

Daleo, P., Ribeiro, P., Iribarne, O., 2003. The SW Atlantic burrowing crab *Chasmagnathus granulatus* Dana affects the distribution and survival of the fiddler crab *Uca uruguayensis* Nobili. J. Exp. Mar. Biol. Ecol. 291:255–267

Dye, A.H., Lasiah, T., 1987. Assimilation efficiencies of fiddler crabs and deposit-feeding gastropods from tropical mangrove sediments. Comp. Biochem. Phys. A. 87, 341-344.

Ens, B.J., Klaassen, N., Zwarts, L., 1993. Flocking and feeding in the fiddler crab (*Uca tangeri*): prey availability as risk-taking behavior. Neth. J. Sea Res. 31, 477–494.

Epifanio, C.E., Little, K.T., Rowe, P.M., 1988. Dispersal and recruitment of fiddler crab larvae in the Delaware River estuary. Mar. Ecol-Prog. Ser. 43, 181-188.

France, R., 1998. Estimating the assimilation of mangrove detritus by fiddler crabs in Laguna Joyuda, Puerto Rico using dual stable isotopes. J. Trop. Ecol. 14, 413-425.

Frith, D.W., Brunenmeister, S. 1980. Ecological and population studies of fiddler crabs (Ocypodidae, genus *Uca*) on a mangrove shore at Phuket Island, western peninsular Thailand. Crustaceana. 39,157-184.

Genoni, G.P. 1985. Food limitation in salt marsh fiddler crabs *Uca rapax* (Smith) (Decapoda: Ocypodidae). J. Exp. Mar. Biol. Ecol. 87, 97-110.

Haines, E.B., Montague, C.L., 1979. Food Sources of Estuarine Invertebrates Analyzed Using ^(13)C/^(12)C Ratios. Ecology. 60, 48-56.

Hartnoll, R.G. 2001. Growth in Crustacea – twenty years on. Hydrobiologia. 449, 111-122.

Hirose, G.L., Negreiros-Fransozo, M.L., 2008. Population biology of *Uca maracoani* Latreille 1802-1803 (Crustacea, Brachyura, Ocypodidae) on the south-eastern coast of Brazil. Panam. J.Aquat. Sci. 3, 373-383.

Hsieh, H.L., Chen, C.P., Chen, Y.G., Yan, H.H., 2002. Diversity of benthic organic matter flows through polychaetes and crabs in a mangrove estuary: $\delta^{13}C$ and $\delta^{34}S$ signals. Mar. Ecol.Prog-Ser. 227, 145-155.

Huettel, A., Ziebis, W., Forster, S., 1996. Flow-induced uptake of particulate matter in permeable sediments. Limnol. Oceanogr. 41, 309–322.

Hughes, C.E., Binning, P., Willgoose, G.R., 1998. Characterization of the hydrology of an estuarine wetland. J. Hydrol. 211, 34-49.

Icely, J.D., Jones, D.A., 1978. Factors affecting the distribution of the genus *Uca* (Crustacea: Ocypodidae) on an east African shore. Estuar. Coast. Mar. Sc. 6, 315-325.

Jennings, A.E., Nelson, A.R., 1992. Foraminiferal assemblage zones in Oregon tidal marshes- relation to marsh floral zones and sea level. J.Foramin. Res. 22, 13-29.

Koch, V., Wolff, M., Dele, K.,2005. Energy budget and ecological role of mangrove epibenthos in the Caeté estuary, North Brazil. Mar. Ecol. Prog-Ser. 228, 119-130.

Koga, T., Backwell, P.R.Y., Christy, J.H., Murai, M., Kasuya, E. 2001. Male-biased predation of fiddler crab. Anim.Behav.62, 201-207.

Koga, T., Backwell, P.R.Y., Jennions, M.D., Christy, J.H.,2015. Elevated predation risk changes mating behavior and courtship in fiddler crabs. Proc. R. Soc. Lond. B 265, 1395-1390.

Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. J. Sea Res. 59, 30-43.

Krumme, U., Keuthen, H., Saint-Paul, U., Villwock, W., 2007. Contribution to the feeding ecology of the banded puffer fish *Colomesus psittacus* (Tetraodontidae) in north Brazilian mangrove creeks. Braz. J. Biol. 67, 383–92.

Lallier-verges, E., Perrussel, B., Disnar, R., Baltzer, F. 1998. Relationships between environmental conditions and the digenetic evolution of organic matter derived from higher plants in a modern mangrove swamp system (Guadeloupe, French West Indies). Org. Geochem.29, 1663-1686.

Luczak, C., Janquin, M., Kupka, A. 1997. Simple standard procedure for the routine determination of organic matter in marine sediment. Hydrobiologia. 345, 87-94.

Machado, G.B.O, Gusmão-Junior, J.B.L, Costa, T.M. 2013. Burrow morphology of *Uca uruguayensis* and *Uca leptodactylus* (Decapoda: Ocypodidae) from a subtropical mangrove forest in the western Atlantic. Integr. Zool. 8, 307–14.

Macintosh, D.J., Ashton, E.C., Havanon, S. 2002. Mangrove rehabilitation and intertidal biodiversity: a study in Ranong Mangrove Ecosystem, Thailand. Estuar. Coast.Shelf S. 33, 331-345.

McWillian, P., Phillips, B.F., 2007. Spiny lobster development: mechanisms inducing metamorphosis to the puerulus: a review. Rev. Fish Biol. Fish.17, 615-632.

Michaels, R.E., Zieman, J.C., 2013. Fiddler crabs (*Uca*spp) burrows have a little effect surrounding sediment oxygen concentration. J. Exp. Mar. Biol. Ecol.448, 104-113.

Miller, D.C., 1961. The feeding mechanisms of fiddler crabs with ecological considerations of feeding adaptations. Zool. Sci. Contrib. N. Y. Zool. Soc.46, 8-100.

Mokhtari, M., Ghaffar, M.A., Usup, G., Cob, Z.C., 2015. Determination of key environmental factors responsible for distribution patterns of fiddler crabs in a tropical mangrove ecosystem. PloS one. 10, 01-17.

Murai, M., Goshima, S., Nakasone, Y. 1983. Adaptive droving behavior observed in the fiddler crab *Uca vocans vocans*. Mar. Biol. 76,159-164.

Nobbs, M., 2003. Effects of vegetation differ among three species of fiddler crabs (*Uca* spp.). J. Exp. Mar. Biol. Ecol. 284, 41–50.

Olabarria, C., Underwood, A.J., Chapman, M.G., 2002. Appropriate experimental design to evaluate preferences for microhabitat: an example of preferences by species of microgastropods. Oecologia. 132,159-166.

Parfilis, P., Meiri, S., Foufopoulus, J.,Valako, E., 2009. Intra-specific competition and high food availability are associated with insular gigantism in a lizard. Naturwissenschaften 96,1107–1113.

Potvin, C., Roff, D., 1993. Distribution-free and robust statistical methods: viable alternatives to parametric statistics. Ecology.74, 1617–1628.

Reinsel, K.A., 2004. Impact of fiddler crab foraging and tidal inundation on an intertidal sandflat: season-dependent effects in one tidal cycle. J. Exp. Mar. Biol. Ecol. 313, 1-17.

Reinsel, K.A., Rittschof D., 1995. Environmental regulation of foraging in the sand fiddler crab *Uca pugilator* (Bosc 1802). J. Exp. Mar. Biol. Ecol. 187, 269-287.

Ribeiro, P.D., Iribarne, O.O., Daleo P., 2005. The relative importance of substratum characteristics and recruitment in determining the spatial distribution of the fiddler crab *Uca uruguayensis* Nobili. J. Exp. Mar. Biol. Ecol. 314:99–111

Rulison, E.L., Luiselli, L., Burke, R.L., 2012. Relative Impacts of Habitat and Geography on Raccoon Diets. Am. Midl. Nat. 168, 231-246.

Sanford, E., Holzman, S.B., Haney, R.A., Rand, D.M., Bertness, M.D., 2006. Larval tolerance, gene flow, and the northern geographic range limit of fiddler crabs. Ecology.87, 2882–94

Seitz, R.D., Lipcius, R.N., Stockhausen, W.T., Delano, K.A., Seebo M.S., Gerde, P.D. 2003. Potential bottom-up control of blue crab distribution at various spatial scales. B. Mar.Sci. 72, 471-490.

Suguio K., 1973. Introdução à sedimentologia, first ed. São Paulo University Press, São Paulo.

Teal, J.M., 1962. Energy flow in the salt marsh ecosystem of Georgia. Bull. Ecol. Soc. Am. 43, 614-624.

Teal, J.M., 1958. Distribution of fiddler crabs in Georgia salt marshes. Bull. Ecol. Soc. Am 39: 186-193.

Thurman, C.L., Faria, S.C., McNamara, J.C. 2013. The distribution of fiddler crabs (*Uca*) along the coast of Brazil: implications for biogeography of the western Atlantic Ocean. Mar. Biodivers. Rec. 6, 01-21.

Underwood, A.J., 1997. Experiments in ecology, first ed. Cambridge University Press, Cambridge

Underwood, A.J., Chapman, M.G., Crowe T.P. 2004. Identifying and understanding ecological preferences for habitat or prey. J. Exp. Mar. Biol. Ecol. 300, 161–187.

Wauters, L.A., Gurnell, J., Preatoni, D., Tosi G., 2001. Effects of spatial variation in food availability on spacing behaviour and demography of Eurasian red squirrels. Ecography. 24, 525-538.

Yang, S.L., Li, H., Ysebaert. T., Bouma, T.J., Zhang, W.X., Wang, Y.Y., Li, P., Li, M., Ding, P.X., 2008. Spatial and temporal variation in sediment grain size in coastal wetlands, Yangtze Delta: on the role of physical and biotic controls. Estuar. Coast. Shelf S. 77, 657–671.

Zar, J.H. 2010. Biostatistical analysis fifth ed. Prentice Hall, Upper Saddle River, New Jersey.

7. Figures

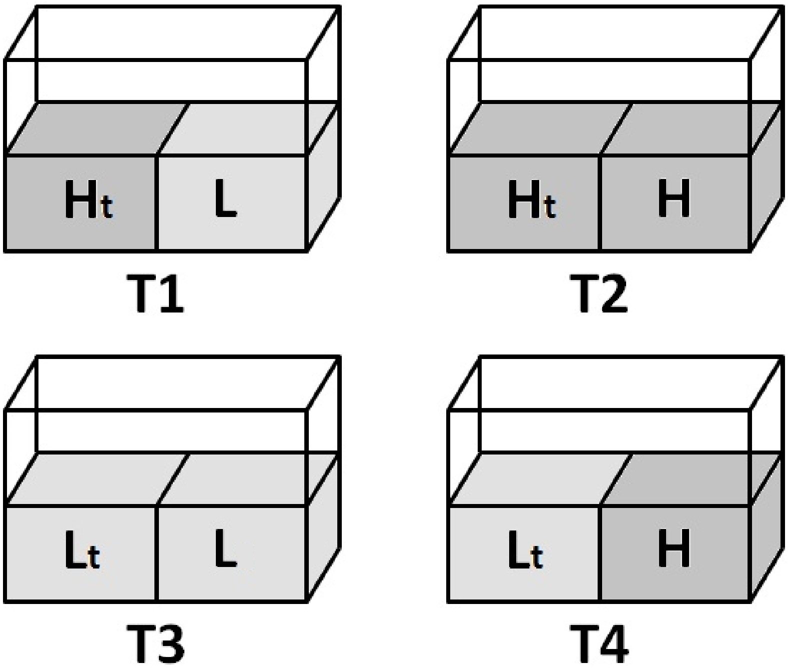

Figure 1: An experimental design overview is shown. Treatments (1-4) used in the experiments to determine *Uca uruguayensis* sediment preference are shown. *H* is high organic content, *L* is low organic content, and *t* indicates the compartment used as reference to compare observed behaviors.

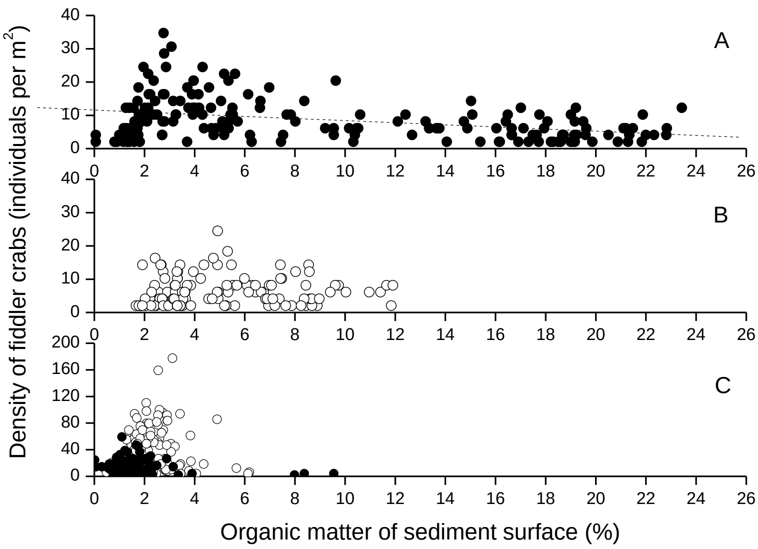

Figure 2. Influences of organic matter on fiddler crab density are shown. Density of fiddler crabs according to percentage of sediment surface organic matter from estuaries at Praia Grande (black circles) and Peruíbe (white circles). A: The relationship between the density of *Uca thayeri* and sediment surface organic content at the Praia Grande estuary is shown. B: The relationship between the density of *Uca thayeri* and sediment surface organic content at Peruíbe is shown. C: Relationship between the density of *Uca Uruguayensis* and sediment surface organic content at Praia Grande and Peruíbe sites is presented.

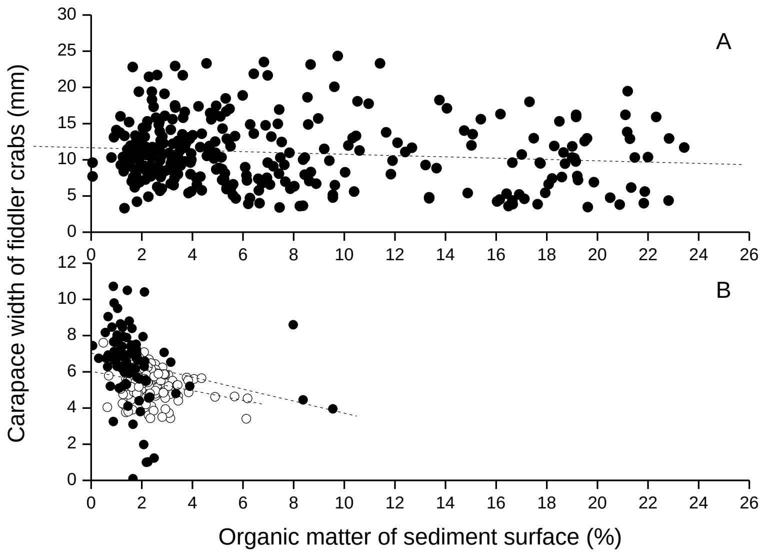

Figure 3: The influence of organic matter on fiddler crab size is shown. A: The relationship between the size of *Uca thayeri* and the surface organic content at Praia Grande and Peruíbe estuaries (combined data) is presented. B: The relationship between the size of *Uca uruguayensis* and sediment surface organic content at estuaries of the Praia Grande (black circle) and Peruíbe (white circle) is presented.

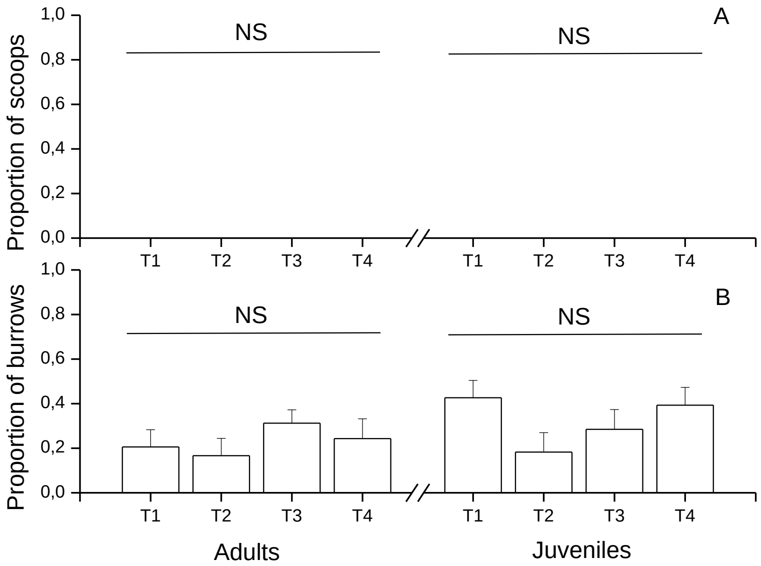

Figure 4. Experiments of preference. The *Uca uruguayensis* does not prefer feed or habitat areas. The error bars represent the mean ±standard error of the proportion (ratio between the two compartments) of scoops and burrows. (A) and habitat (B), respectively. T1…T4 is the treatments (see figure 1for more details), NS indicate no difference among treatments.

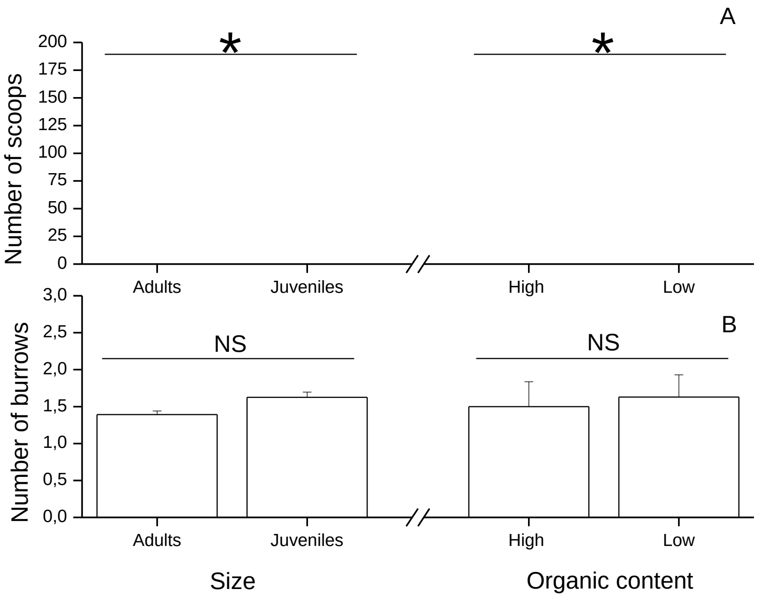

Figure 5. Sediment ingestion and burrows dug by *Uca uruguayensis* are shown. Error bars represent the mean ± standard error of total scoops (A) and burrows dug (B) by adults and juveniles of *Uca uruguayensis* (left), and both sizes in sediments with high and low organic contented treatments (right). The "*" indicates a significant difference and "NS" indicates no significant differences