UNIVERSIDADE FEDERAL DO PARÁ
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
EMBRAPA AMAZÔNIA ORIENTAL
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

DIEGO GARCIA CORDEIRO SOUZA

Ecologia populacional de *Ocypode quadrata* (Brachyura: Ocypodidae) em uma praia arenosa exposta de macromaré da costa amazônica do Brasil

Belém

2017

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia do convênio da Universidade Federal do Pará e Embrapa Amazônia Oriental, como requisito parcial para obtenção do título de Mestre em Ecologia.
Área de concentração: Ecologia.
Linha de Pesquisa: Ecologia de Organismos e Populações.

Orientador: Prof. Dr. Marcelo Petracco
(PPGECO/UFPA)
Coorientadora: Profa. Dra. Maíra Pombo
(PPGBio/UNIFAP)

Belém
2017

Dados Internacionais de Catalogação na Publicação (CIP) de acordo com ISBD
Sistema de Bibliotecas da Universidade Federal do Pará
Gerada automaticamente pelo módulo Ficat, mediante os dados fornecidos pelo(a) autor(a)

C794e Cordeiro Souza, Diego Garcia
Ecologia populacional de Ocypode quadrata (Brachyura: Ocypodidae) em uma praia arenosa exposta de macromaré da costa amazônica do Brasil / Diego Garcia Cordeiro Souza. — 2017.
ix, 48 f. : il.

Orientador(a): Prof. Dr. Marcelo Petracco
Coorientação: Prof^{a}. Dra. Maíra Pombo
Dissertação (Mestrado) - Programa de Pós-Graduação em Ecologia, Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, 2017.

1. Ocypode. 2. Amazônia. 3. Praias. 4. Ecologia costeira. 5. Oceanografia. I. Título.

CDD 578.7699

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Ao meu finado pai, Arlindo Pinto de Souza Júnior, por instigar em mim o fascínio pelas ciências e pelo mundo natural desde a tenra idade. À minha mãe, Dineia Cordeiro Souza, e irmã, Daniele Garcia Cordeiro Souza, por estarem ao meu lado, inspirando-me e animando-me sempre.

AGRADECIMENTOS

Aos orientadores Marcelo Petracco e Maíra Pombo pelo apoio, críticas e sugestões fornecidos ao longo do mestrado, sem os quais o presente trabalho não seria possível. Ao Dr. José Eduardo Martinelli Filho, pelos comentários e auxílio de campo.

À todos os amigos do Laboratório de Oceanografia Biológica e de minha turma de graduação em Ciências Biológicas, por todo o apoio pessoal e em campo, e os muitos bons momentos vividos no decorrer da pós-graduação, especialmente: Alysson Leite, Ana Paula Danin, Arianderson Silva, Arnaldo Fabrício, Ayrton Leal Carvalho, Bruno Simi, Daiane Aviz, Denys Costa, Felipe “Barba” Souza, Gabriel Soares, Leonardo Morais, Mayara Cardoso, Mayk Almeida, Roseanne Figueira, Santino Neto, Stéfany Mattos e Thuareag Monteiro. Um obrigado também a Álvaro Luan, Carlos Bacellar e Rômulo Gabriel Rodrigues.

À amigos e mentores do Museu Paraense Emílio Goeldi (MPEG) pelas conversas e aprendizado, em especial ao amigo César Favacho. Agradecimentos muito especiais aos doutores William Leslie Overal e Inocêncio de Sousa Gorayeb, pessoas excepcionais cujo profundo conhecimento do mundo natural inspiram admiração cada vez maior pela ciência da Biologia. Um obrigado ao Dr. Ivanei Souza Araújo, pelo apoio e incentivo em ingressar no mestrado.

À equipe docente do Instituto de Ciências Biológicas da UFPA e do Programa de Pós-Graduação em Ecologia, pela formação e aprendizado. Ao Prof. Dr. Leonardo dos Santos Sena, quem, no início da graduação, primeiro nos ensinou a pensar como cientistas.

À CAPES, pela oferta de bolsas indispensáveis no desenvolvimento dos trabalhos de campo.

À minha família, presente ao longo de todo o percurso. Pelo suporte em minha vida pessoal, pelo alicerce em horas de dificuldade e sinergia em momentos de alegria.

Epígrafe

Nothing in life is to be feared, it is only to be understood. Now is the time to understand more, so that we may fear less.

Marie Skłodowska Curie (1867 – 1934)

Ecologia populacional de *Ocypode quadrata* (Brachyura: Ocypodidae) em uma praia arenosa exposta de macromaré da costa amazônica do Brasil

RESUMO

Este trabalho propõe-se a analisar aspectos da ecologia populacional da espécie *Ocypode quadrata* (Brachyura: Ocypodidae) em uma praia arenosa exposta, dissipativa e de macromaré situada no nordeste do estado do Pará, Brasil, no período de um ano. A população foi amostrada por métodos indiretos (contagem e mensuração de tocas) e diretos (escavação das tocas e análise dos indivíduos). Analisou-se a variação na abundância das tocas ao longo do tempo e em função de variáveis ambientais relevantes em ambientes de praia e na região (propriedades do sedimento, precipitação, temperatura do ar e água do mar e salinidade). Descreveu-se a zonação a partir da distribuição das tocas em relação à distância da linha de maré alta. O diâmetro das tocas foi aplicado na estimativa de parâmetros de crescimento individual da população. Estimou-se a taxa de ocupação das tocas, razão sexual e relação entre diâmetro da toca e medidas dos indivíduos (largura, comprimento e largura da carapaça). Houve diferença na abundância entre as duas estações amazônicas, sendo maior na estação chuvosa (0,78 ± 0,24 tocas.m^{-1}) que na de estiagem (0,37 ± 0,13 tocas.m^{-1}). Houve influência apenas de precipitação e tamanho do grão do sedimento arenoso. A população praticamente restringiu-se ao supralitoral da praia. Os parâmetros de crescimento individual estimados (L_∞=53,36 mm, K=0,76 yr^{-1}, t_0=0,014 yr, Φ=3,34) descrevem uma curva com bom ajuste à progressão temporal das coortes. A ocupação das tocas variou entre 12,5% a 28,7%. A razão sexual manteve equilíbrio na estação chuvosa, com mudança para predominância de machos na estiagem. O diâmetro das tocas relacionou-se sobretudo com a largura da carapaça. Essas são informações iniciais sobre o comportamento de *Ocypode quadrata* em ambientes amazônicos de macromaré. Quando comparadas com dados de outras regiões, fornecem *insights* sobre tendências latitudinais de parâmetros populacionais.

Palavras-chave: *Ocypode*, Amazônia, Praias arenosas, Ecologia costeira, Oceanografia.

Population ecology of *Ocypode quadrata* (Brachyura: Ocypodidae) on an exposed macrotidal sandy beach of the Brazilian Amazon coast

ABSTRACT

The present study analyzes the population ecology of *Ocypode quadrata* (Brachyura: Ocypodidae) on an exposed, macrotidal, dissipative sandy beach located on the Amazon coast, during one year. Indirect (burrow counting and measurement) and direct (burrow excavation and assessment of individuals) methods were used on population assessments. Burrow abundance variation was analyzed over time and as a function of environmental variables (sediment properties, precipitation, air and seawater temperature, salinity). Zonation was described through burrow distribution by distance from the high tide mark. Burrow diameter was used to estimate individual growth parameters of the population. Burrow occupation rate, sex ratio and relation between burrow diameter and crab measures (carapace length, width and depth) were also estimated. Abundance was higher on the rainy season (0.78 ± 0.24 burrow.m^{-1}, against 0.37 ± 0.13 burrow.m^{-1} on the dry season) and related positively to precipitation and negatively to sediment grain size. The population was practically restricted to the supralittoral zone. The estimated individual growth parameters (L_∞=53.36 mm, K=0.76 yr^{-1}, t_0=0.014 yr, Φ=3.34) describe a well-adjusted curve to cohort progression over time. Burrow occupation rate varied between 12.5% and 28.7%. There was sex equilibrium during the rainy season, however, changing to male predominance on the dry season. Burrow diameter was related mainly to carapace width. These are the first data of ghost crab population behavior on Amazon macrotidal environments. These, compared to available data on other regions, also gives insight on latitudinal tendencies of population parameters.

Keywords: Palavras-chave: *Ocypode*, Amazon, Sandy beaches, Coastal ecology, Oceanography.

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SUMÁRIO

INTRODUÇÃO GERAL

As praias arenosas são ambientes extremamente dinâmicos, de interface entre terra e água, com substrato de sedimentos inconsolidados. A estrutura física predominante do habitat é determinada pela interação de três fatores principais: marés, ondas e tipo de sedimento (Short and Wright, 1983; Defeo and McLachlan, 2005). A variação destes fatores físicos e geológicos molda a topografia local, resultando em um gradiente de praias distintas, classificadas em estados morfodinâmicos. Estes estados variam entre um extremo refletivo e outro dissipativo. O estado refletivo é característico de condições de micromarés (< 2m) e ondas de baixa energia que quebram diretamente na face praial, tendo a energia refletida de volta para o mar. Praias desse tipo tendem a possuir maior declividade e sedimento grosso. O estado dissipativo surge geralmente em condições de macromarés (> 4 m) e ondas de alta energia, havendo uma zona de surfe onde as ondas dissipam a maior parte de sua energia. Essas praias normalmente possuem topografia mais plana e sedimentos finos (Short and Wright, 1983; Defeo and McLachlan, 2005; McLachlan and Brown, 2006). Esta variedade de ambientes pode gerar composições distintas da macrofauna de praias, devido ao fato das espécies serem dotadas de diferentes adaptações e faixas de tolerância concernentes às condições físicas predominantes em cada tipo morfodinâmico (Defeo and McLachlan, 2005). O entendimento de padrões de variação da macrofauna é essencial para o entendimento da dinâmica natural dos ecossistemas de praias, bem como o seu efetivo manejo e conservação.

Várias hipóteses buscam explicar a variação dessas espécies segundo o estado morfodinâmico (McLachlan et al.,1993; Defeo and McLachlan, 2005, 2013; Nel et al., 2014). Dessas, duas hipóteses principais fazem predições a nível de populações de seres vivos. A Hipótese da Severidade Ambiental (HHH – Habitat Harshness Hyphothesis) (Defeo and Martínez, 2003) propõe que praias refletivas constituem um ambiente rigoroso para a macrofauna e leva os indivíduos a investir mais energia na sua manutenção (sobrevivência). Dessa maneira, espera-se que populações que habitam praias refletivas apresentem menores valores de abundância, fecundidade e taxas de crescimento e sobrevivência. Essas asserções são verdadeiras sobretudo para organismos da zona entremarés, como espécies dos gêneros *Donax* e *Emerita*, uma vez que a rigorosidade ambiental advém sobretudo da quebra das ondas diretamente sobre a face praial e subsequentes espraiamentos turbulentos (Defeo et al., 2001; Brazeiro, 2005; Celentano and Defeo, 2006; Petracco et al., 2016). A Hipótese da Segurança do Habitat (HHS – Hyphothesis of Habitat Safety), por outro lado, prediz que para formas do supralitoral, como anfípodes talitrídeos, são observadas tendências inversas, pois maiores inclinações da praia resguardam esses organismos das ondas e espraiamento (Defeo and Gómez, 2005). Existem, também, variações de parâmetros populacionais em escala latitudinal. Para crustáceos, por exemplo, ocorrem tendências de diminuição de abundância e tamanho máximo, e de aumento em taxas de crescimento de mortalidade, de praias temperadas a tropicais (Cardoso and Defeo, 2003; Defeo and Cardoso, 2004; Defeo and McLachlan, 2005; Petracco et al., 2010).

Uma das mais conspícuas espécies da macrofauna de praias arenosas são os caranguejos do gênero *Ocypode* (Brachyura: Ocypodidae), popularmente conhecidos no Brasil como “guaruçá” ou “maria-farinha”. São encontrados em regiões tropicais e subtropicais de todo o mundo (McLachlan and Brown, 2006), constituindo componentes importantes dos ambientes praiais. Atuam como predadores, detritívoros e depositívoros e podem tanto reduzir matéria orgânica quanto atuar no controle *top-down* desses ecossistemas (Wolcott, 1978; Robertson and Pfeiffer, 1981; Tewfik et al., 2016). Distribuem-se desde a zona entremarés até o supralitoral e dunas arenosas, onde cavam tocas individuais semi-permanentes (Souza and Gianuca, 1995; Branco et al., 2010). O recrutamento dos juvenis ocorre com o assentamento de larvas megalopas na face praial. Juvenis passam então a habitar o substrato arenoso da zona entremarés (Lucrezi and Schlacher, 2014), podendo estar limitados a áreas próximas da água devido a capacidades de movimentação e escavação limitadas. Isso pode levar a tendência de estratificação da distribuição da população, com indivíduos maiores e mais velhos ocupando áreas mais distantes (Milne and Milne, 1946; Branco et al., 2010; Lucrezi, 2015). Há relação direta entre diâmetro das tocas e tamanho dos indivíduos (Turra et al., 2005; Oliveira et al., 2016), o que permite a amostragem indireta de populações, por meio de censos e mensurações das tocas (Pombo, 2015). Esta relação torna o gênero *Ocypode* um grupo interessante para estudos concernentes à dinâmica natural de ecossistemas praiais, além um recurso para o rápido monitoramento desses ambientes (Barros, 2001; Lucrezi et al., 2009; Lucrezi, 2015; Schlacher et al., 2016).

Porém, as respostas populacionais de *Ocypode* a diferentes estados morfodinâmicos, bem como suas predições de acordo com hipóteses existentes, ainda são tema de debate. Resultados contrastantes podem ser encontrados na literatura. Por exemplo, menores densidades populacionais de *O. quadrata* foram associadas a sedimentos finos e fracamente selecionados no sudeste brasileiro (Turra et al., 2005), enquanto não se observaram relações entre densidades de *O. gaudichaudii* e atributos morfodinâmicos no norte do Chile (Quijón et al., 2001). Ainda, estudos mais recentes mostram que populações de *O. quadrata* beneficiam-se tanto em condições de ambientes dissipativos quanto refletivo, em parte discordando de ambas HHH e HHS (Lucrezi and Schlacher, 2014; Pombo, 2015; Pombo et al., 2017). *O. quadrata* é a única espécie do gênero presente na costa atlântica dos continentes americanos, talvez sendo também a de maior amplitude geográfica (Sakai and Türkay, 2013). Isto a torna interessante para análises comparativas entre ambientes distintos tanto morfodinamicamente quanto latitudinalmente. Estudos com a espécie foram conduzidos principalmente nos Estados Unidos (Wolcott, 1984; Wolcott and Wolcott, 1985; Weinstein et al., 1994; Hobbs et al., 2008; Tewfik et al., 2016) e Brasil (Negreiros-Fransozo et al., 2002; Neves and Bemvenuti, 2006; Rosa and Borzone, 2008; Branco et al., 2010; Pombo and Turra, 2013; Pombo, 2015; Oliveira et al., 2016), contudo geralmente restritos a praias de micromarés. Latitudinalmente, sua distribuição ainda possui regiões de potencial estudo, sendo os trabalhos mais próximos da linha equatorial aqueles conduzidos por Valero-Pacheco et al. (2007) (18°39’ N) e Souza et al. (2008) (7°51’ S). Uma melhor compreensão da interação entre essas populações e seu ambiente físico ainda é necessária para seu uso adequado como ferramenta de monitoramento de ecossistemas costeiros. Estudos de *O. quadrata* em ambientes praiais variados, distintos tanto morfodinamicamente quanto geograficamente, podem auxiliar a obtenção desse conhecimento.

Esta dissertação de mestrado descreve o primeiro estudo da dinâmica populacional de *O. quadrata* em uma praia arenosa exposta, dissipativa e sob regime de macromarés situada na região costeira da Amazônia. A população estudada é sujeita a características ambientais singulares, incluindo temperaturas altas e constantes ao longo do ano, sazonalidade marcada por um período de alta precipitação seguido por outro de baixa precipitação e marés altas de até 7,5 metros. Os dados adquiridos trazem informações novas para a compreensão da ecologia da espécie. Para tanto, buscou-se uma avaliação geral da população, dividida em dois objetivos principais. Ao longo de um ano, através de amostragem indireta (contagem e mensuração das tocas), examinou-se a abundância e a distribuição das tocas na praia ao longo de um ano, analisou-se o efeito de diferentes variáveis ambientais (características do sedimento, precipitação, temperaturas do ar e água do mar, salinidade) sobre a abundância e estimou-se parâmetros de crescimento individual na população. Segundo, por amostragem direta dos indivíduos, estimou-se a taxa de ocupação das tocas, a razão sexual e a relação entre o diâmetro das tocas e o tamanho de seus ocupantes. Ambas abordagens metodológicas possuem méritos para estudos populacionais e análises de qualidade ambiental utilizando essa espécie.

Os dados obtidos neste trabalho, analisados tanto no contexto local quanto comparados a informações de outras regiões, ampliam o conhecimento da dinâmica populacional da espécie. Localmente, se observam efeitos provenientes de mudanças ambientais características das estações climáticas do bioma amazônico, notadamente aquelas geradas pelo alto regime de precipitação da estação chuvosa. A comparação dos resultados com outros obtidos em diferentes áreas mostra que características locais são mais importantes que fatores latitudinais.

Population ecology of *Ocypode quadrata* (Brachyura: Ocypodidae) on a exposed macrotidal sandy beach of the Brazilian Amazon coast

Diego Garcia Cordeiro Souza[a*], Maíra Pombo[b], Marcelo Petracco[a], José Eduardo Martinelli Filho[a]

[1] *Laboratório de Oceanografia Biológica, Instituto de Geociências, Universidade Federal do Pará, Pará, Brazil.*

[2] *Instituto Oceanográfico, Universidade de São Paulo, São Paulo, Brazil.*

* Corresponding author.

E-mail address: diego00alfa@gmail.com (DGCS)

Abstract

Ocypodid crabs (Brachyura: Ocypodidae) are important components of sandy beach ecosystems and potential indicators of environmental stress. While the genus *Ocypode* is globally dispersed, it is still discussed how their populations respond to distinct beach morphodynamics. We assess an *Ocypode quadrata* population, the only *Ocypode* species present on American Atlantic coasts, on an exposed macrotidal dissipative beach on the Amazon coast. This is the first *O. quadrata* study on the Amazon, the closest to the equatorial line so far. We investigate burrow abundance trends over a year period, responses to major physical factors (sediment, precipitation, air and seawater temperature and seawater salinity), estimate individual growth parameters and perform a descriptive analysis of burrow zonation. By direct crab assessments, we estimate burrow occupation rate, sex ratio and the relation between burrow and crab measures. We compare our results to available data on other latitudes. Burrow abundance had marked differences among Amazon's rainy and dry seasons and was significantly modeled by precipitation and sediment grain size. Abundance do not show clear latitudinal trends, while density appears to be lower on the tropics. Burrows were present almost exclusively on the supralittoral zone. Estimated growth parameters do not show any latitudinal pattern, being more variable among distinct beaches rather than over large geographical areas. We found low burrow occupation rate, higher male proportion and a significant relation between burrows diameter and crab carapace width. Our study show novel information on *O. quadrata* ecological patterns, highlighting the population behavior on the peculiar environment presented on Amazon coasts.

1. Introduction

Sandy beaches are very dynamic systems, where the interaction between sediment, waves and tides generates different beach profiles (Short, 1996; Defeo and McLachlan, 2005). This interplay shapes the beach topography, resulting in a continuum of environments with characteristic slopes and physical attributes, classified in several morphodynamic types. Beaches vary from reflective (steeper beaches with coarser sediments) to dissipative states (flatter beaches with finer sediments) (Short, 1996). This environmental variation can lead to different macrofauna compositions, since each beach species has distinct adaptations and tolerance ranges to the physical stress (Defeo and McLachlan, 2005). As such, several hypotheses attempt to explain and predict resulting patterns of change in macrofauna biological descriptors (McLachlan et al., 1993; Defeo and McLachlan, 2005, 2013; Nel et al., 2014). On the population level, the Habitat Harshness Hypothesis (HHH) (Defeo et al., 2001; Defeo and Martínez, 2003) successfully predict that the harsh environment of reflective beaches, due mainly to waves breaking directly over the steep beach face and turbulent swashes, prompts truly intertidal organisms, such as *Emerita* and *Donax species,* to diverge energy towards maintenance, inducing lower values of population abundance, fecundity, and growth and survival rates (Defeo et al., 2001; Brazeiro, 2005; Celentano and Defeo, 2006; Petracco et al., 2016). Conversely, for supralittoral species such as talitrid amphipods (Defeo and Gómez, 2005), the Hypothesis of Habitat Safety (HHS) (Defeo and Gómez, 2005) proposes an opposite trend, where steeper slopes benefit supralittoral forms by functioning as shelter from the swash. Important beach macrofauna trends were reported also on a latitudinal scale (Defeo and McLachlan, 2005) including, for crustaceans, decrease of abundance and maximum length, and higher mortality and growth rates from temperate to subtropical populations (Cardoso and Defeo, 2003, 2004; Defeo and McLachlan, 2005; Petracco et al., 2010). Understanding macrofaunal trends is important for accurate predictions regarding environmental changes on sandy beach environments and for effective management efforts, especially in the light of shore alterations resulting from climate change and intense urbanization processes (Brown and McLachlan, 2002; Defeo et al., 2009; Turra et al., 2013)[.

One of the most conspicuous and widespread macrofauna invertebrates from coastal ecosystems are Ocypodid crabs (Brachyura: Ocypodidae) (McLachlan and Brown, 2006; Lucrezi and Schlacher, 2014). The genus *Ocypode* is globally dispersed, present on the upper-intertidal and supralittoral zones of sandy beaches on the tropics and subtropics (McLachlan and Brown, 2006; Sakai and Türkay, 2013). The species *Ocypode quadrata* (F.) is the only one present on the Atlantic coast of the Americas. Along with other ghost crabs, they are important links on the food web, acting as predators, scavengers and deposit-feeders, both reducing organic matter and operating in top-down control on the beach ecosystem (Wolcott, 1978; Robertson and Pfeiffer, 1981; Tewfik et al., 2016). They excavate individual burrows, which can be used as a useful proxy for rapid assessments (Neves and Bemvenuti, 2006; Lucrezi et al., 2009; Schlacher et al., 2016). However, it is still discussed how *Ocypode* populations respond to morphodynamics, and whether such responses can be predicted by existing hypotheses. Different behaviors were reported, e. g. lower densities of *O. quadrata* were associated with very fine and poorly sorted grains on southeast Brazil (Turra et al., 2005), while no clear relationships between *O. gaudichaudii* densities and morphodynamic features were observed in northern Chile (Quijón et al., 2001). Recent studies with *O. quadrata* agree in what it seems to benefit from steeper slopes, but also showing to be more abundant towards dissipative conditions, therefore somewhat diverging from the predict by both the HHH and HHS (Lucrezi 2015; Pombo et al., 2017). Robust knowledge of population biology and adequate use of *O. quadrata* populations as a monitoring tool of sandy shore ecosystems requires correctly understanding the interaction between crab populations and their physical environment, better achieved by surveying on a wide variety of beaches and latitudes.

The present study assessed several ecological parameters for an *O*. *quadrata* population in a preserved exposed macrotidal dissipative sandy beach, located in the Brazilian Amazon coast (equatorial latitude). The studied population is subject to peculiar environmental features as high and almost constant temperature over the year, presence of very wide intertidal and supralitoral zones and a precipitation regime with two well-marked periods. Therefore, this study broadens the understanding of this ghost crab ecology in relation to an unprecedented set of characteristics, of global relevance. Because of the lack of knowledge in such conditions, a broad population assessment was performed and divided into two main objectives. First, using an indirect method by counting and measuring the burrows we assess the abundance and across-shore distribution over dates and seasons, the relationship of abundance with environmental variables (air temperature, precipitation, sand particle size and seawater temperature and salinity) and estimate the body growth parameters. Second, through direct crab measurements, we estimate burrow occupation rate, sex ratio and the relation between crab and burrow sizes. Both ecological approaches are, in different ways, relevant to assess environmental quality, so the peculiarities of this environment will support such assessments in a broader scale.

2. Methodology

2.1. Study area

Corvinas beach (0°36'17.2"S; 47°23'04.7"W to 0°36'14.6"S; 47°22'04.4"W) is a sandy beach located at the Amazon Coast, Northern Brazil (Salinópolis/Pará; Fig 1). It is a preserved and exposed and dissipative beach, whose morphodynamic state varies slightly between two marked seasons: from dissipative state on the rainy one (January to June, $\Omega > 5.5$; mean precipitation 330 mm/month) to longshore bar and trough on the dry one (July to December, $4.7 < \Omega < 5.5$; mean precipitation 50 mm/month) (Fisch et al., 1998; Moraes et al., 2005; Reboita et al., 2010; Ranieri, 2014; Ranieri and El-Robrini, 2015). The rainy season lasts on January-June and the dry season July-December on the Salinópolis region, with overall precipitation above 2000 mm per year (Moraes et al., 2005). Sediment grain size is very fine (2.6 to 2.8 phi) (Ranieri, 2014; Ranieri and El-Robrini, 2015). The intertidal zone is very wide, reaching up to 1 km on spring tides (personal observations), with slope not exceeding 1.5° (Ranieri, 2014). The beach is bordered by low-height vegetated dunes followed by a mangrove. Local weather is wet/dry tropical, with 26 °C annual mean air temperature (Fisch et al., 1998). A macrotidal regime is defined by semi-diurnal tides ranging from 4 to 5.3 m (Souza Filho, 2005; Ranieri, 2014; Ranieri and El-Robrini, 2015). Mean wind velocity on the area is 4.10 $m.s^{-1}$ varying mainly on directions between 20 and 30°, and waves are up to 0.7 m high Ranieri, 2014; Ranieri and El-Robrini, 2015.

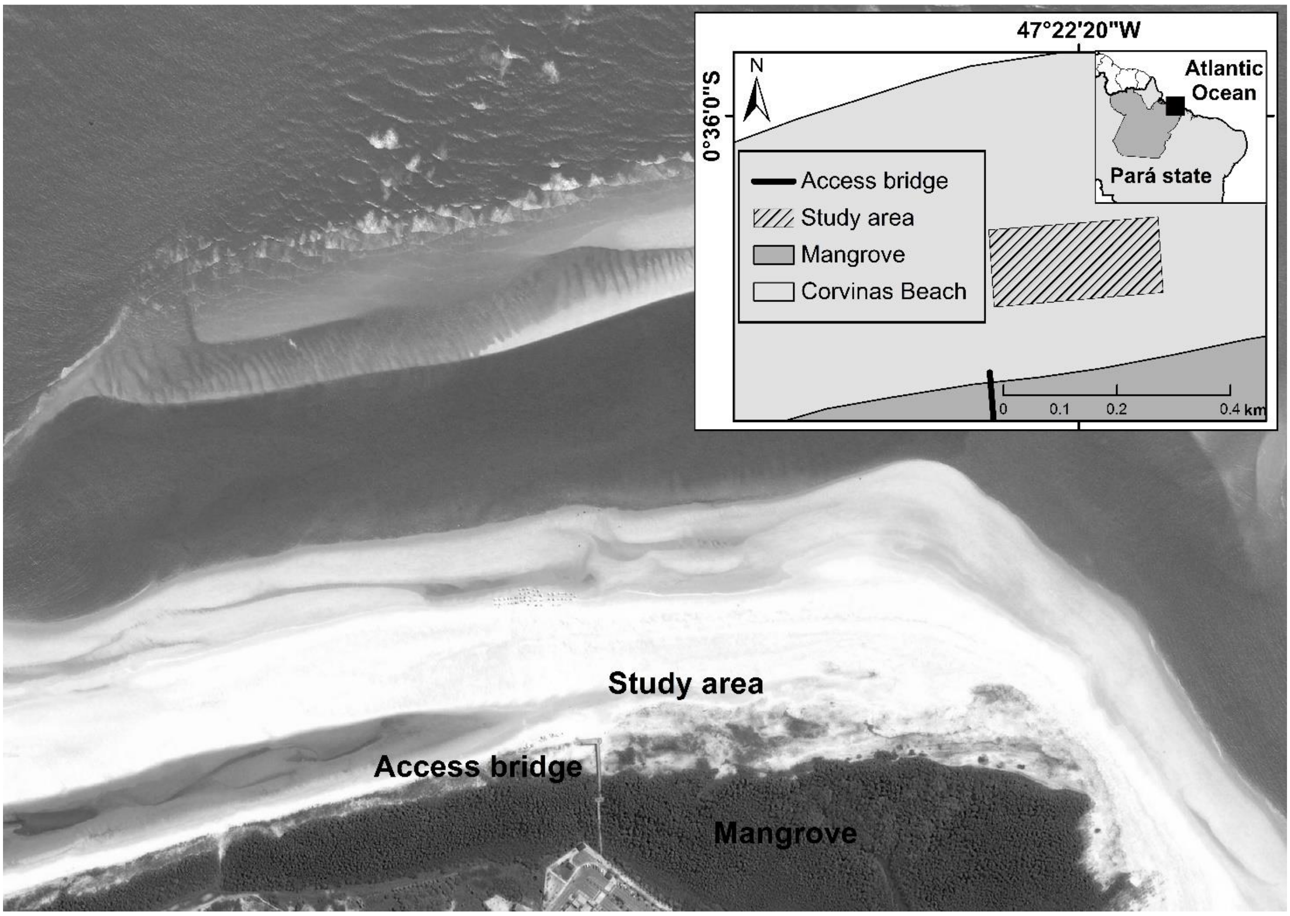

Fig. 1. Map of Corvinas beach, detailing the study area, access bridge and surrounding mangrove. Satellite imagery from Google Earth Pro V 7.1.5.1557 (May 7, 2010). 0°36’14.4”S, 47°22’26.4”W, Eye alt 1.47 km. Digital Globe 2016. https://www.google.com/earth [February 21, 2016].

2.2. Sampling procedures

Field samples were conducted monthly during spring tides, from November 2015 to October 2016. To avoid noises from adjacent systems, a homogeneous 300 m alongshore section was selected, measured from a fixed point (0°36’14.4”S; 47°22’26.4”W). Within this area, five transects perpendicular to the water line were randomly placed. Each transect was 20 m wide and had a varying length, from the first (seaward) to the last (landward) burrow observed, covering the whole across-shore range of occurrence of burrows.

Six physical factors were assessed. Granulometry, for which a total of three sediment samples were monthly taken, comprising three strata: beginning, middle and end of the range of occurrence of burrows. Since transects covered the whole range of occurrence, we took sand samples inside the largest one. Sediment particle size and sorting coefficient were obtained through procedures described by Suguio (1973), in phi-units (φ). Values from the three strata were averaged, characterizing the whole range of occurrence at each sampling date. Granulometry could not be assessed on March 2016. Water temperature and salinity were measured *in situ* with digital thermometer and optical refractometer, respectively. Air temperature and rainfall were gathered online at INMET portal (acronym for, in Portuguese, *Instituto Nacional de Meteorologia* - http://www.inmet.gov.br); from the Salinópolis weather station (Salinópolis-A215). Since both data is gathered daily, each month we estimated a mean value for the interval between the sampling date and the day right after the previous sample. Additionally, the range of occurrence of burrows was measured monthly as the mean (m) length of all transects, resulting on an average measure of the across-shore distance inhabited by ghost crabs.

Ghost crabs were indirectly assessed by counting and measuring all burrows inside the transect area. Diameter was measured with a caliper rule at the bottom of the funnel-shaped upper portion of the burrows (Pombo and Turra, 2013), avoiding superficial sediment deformations that could distort the relationship between diameter and crab size. Across-shore distribution was assessed by counting burrows every 10 meters inside the transect, thus detailing abundance and size disposal along the range of occurrence. We also measured distances between transects and the high tide mark, giving a perspective of range of occurrence position on the beach, and standardizing relative burrow distances to the high tide mark. This means that burrows were counted at set distances to the drift line, regardless of range of occurrence position on the beach.

Direct assessments of crabs were performed on March, June and September 2016. This direct approach consisted in the excavation of the burrows after the above procedures. A flexible steel cable was inserted to the bottom of the burrows and used as a guide to the excavation. This process was performed manually, probing around so as to locate eventual burrow ramifications, until the bottom was reached. The burrow was classified either as unoccupied or occupied, in which case the crab was captured, sexed and measured (carapace length, width and height).

2.3. Data analysis

Burrow abundance was measured in occurrences per strip transect (burrows.m^{-1}) (Defeo, 1998), obtained by dividing the total number of burrows within a transect by its width (20 m). Mean abundance was compared between seasons and the sampling dates within each season using a two-way nested ANOVA, so as to assess the main factor driving differences in population size throughout time. Data was base 10 log-transformed to meet all the ANOVA assumptions, which was followed by a post-hoc Tukey test. The relationship between burrow abundance and environmental variables was assessed using a stepwise forward multiple linear regression, after checking for data normality and collinearity between factors and followed by the analysis of residuals to ensure that homogeneity and homoscedasticity assumptions were met. Data from March 2016 was disregarded on the multiple regression only, to avoid missing granulometry data.

A descriptive assessment of *O. quadrata* zonation regarding abundance and size was performed by season, considering the burrow distances to the drift line. For this purpose, burrows were classified as from a juvenile (<20 mm) or adult crab (>20 mm) (Negreiros-Fransozo et al., 2002) and counted every 10 m section from the latest high tide drift line. Mean length (m) of the interval between the drift line and the range of occurrence (first and last observed burrows) indicated whether the crab's occurrence area shifted seaward or landward over time.

For growth analysis, burrow diameter was grouped in 5 mm classes as performed by Pombo (2015). An age-size key was built by calculating the means of the main size modes in each month, and identifying their progression over time. The settlement age, in years, was used to estimate an age for the lowest size class (Diaz and Costlow, 1972). Further size classes were aged by summing up progressively the respective intervals (also in years) between sampling dates. These values were used to parameterize the von Bertalanffy growth model (VBGM), with consequent estimates of asymptotic length (L∞), growth constant (K), theoretical age at zero length (t_0), seasonal growth oscillations (C) and winter-point (period of growth reduction, WP), according to the function:

$$L_t = L_\infty \left\{1 - e^{[-k(t-t_0)-KC/2\pi * sen2\pi(t-WP)+KC/2\pi * sen2\pi(t-WP)]}\right\}$$

Length classes frequencies were then used to build monthly histograms across which the graphs of the parameterized VBGM were added to all identifiable cohorts, by means of the ELEFAN I package of the FISAT II program (Gayanilo et al., 2005). The growth performance index (phi-prime) was estimated according to the formula logK + 2logL∞ (Pauly and Munro, 1984).

Occupation rate was estimated for each direct assessment date, by dividing the number of crabs captured within a transect by the respective number of burrows. Sex ratio was tested against a 1:1 ratio through a chi-squared (x^2) test considering the different seasons. Crab body measures (carapace length, width and height) were individually used in linear regressions to investigate which one was better related to burrow diameter. In September 2016, due to the small number of individuals excavation was extended along the whole study area. This additional data was used in analysis of occupation rate, sex ratio and relationship between burrow and individual sizes only.

3. Results

3.1. Environmental factors

Mean particle size was 2.62 ± 0.12 φ for the entire period, being slightly higher on the dry season (2.64 ± 0.14 φ versus 2.59 ± 0.08 φ on the rainy season). Sorting coefficient showed an inverse trend, slightly higher on the rainy season (0.36 ± 0.05 φ, against 0.32 ± 0.07 φ on dry season; mean 0.34 ± 0.07 φ on the whole period), i.e., the beach was characterized by fine, well sorted sand (Fig. 2A and 2B). Total precipitation was 1691.6 mm with great variation among seasons. The rainy season accounted for approximately 85% of rainfall, while the dry season had months of nearly zero precipitation (Fig 2C). Seawater salinity followed a trend inverse to precipitation (Fig 2D), with lowest value of 17 on April

2016 (rainy season) and a highest of 40 on September, October and November (dry season). Mean salinity was 33.17 ± 5.8 ‰ overall, 38.67 ± 2.82 on the dry season and 27.67 ± 4.44 ‰ on the rainy season. Air temperature was stable, not exceeding a range of 1.5°C, being highest on December 2015 (29°C ± 1.2) and lowest on March 2016 (27.2°C ± 1.2) (Fig 2E). Seawater temperature was also stable, within a 5°C range and with a mean of 28.7°C ± 1.1 along the year (Fig 2F). Length of the burrow range of occurrence, on the other hand, varied considerably, from 10 ± 0.0 m on Sep 2016 to 104 ± 7.2 m on Jan 2016. Mean of the range of occurrence on the rainy season was 68 ± 14 m and on the dry season 61.8 ± 23.3 (Fig 2G).

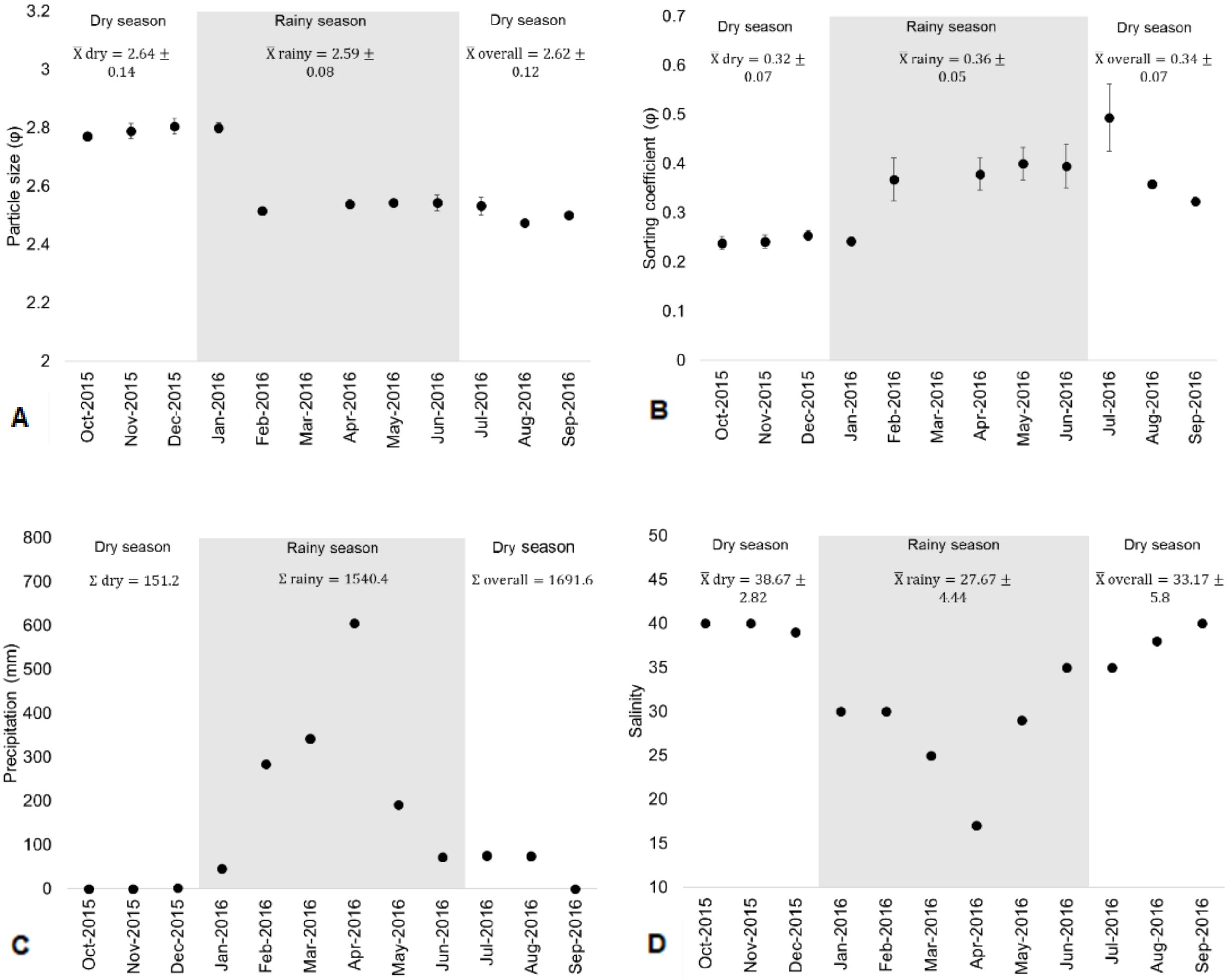

Fig. 2. Physical factors and length of the range of occurrence of *Ocypode quadrata* sampled on Corvinas beach, Salinópolis, Brazil. (A) Mean sediment particle size. (B) Mean sorting coefficient. (C) Precipitation. (D) Salinity. Whiskers indicate standard deviation of the mean.

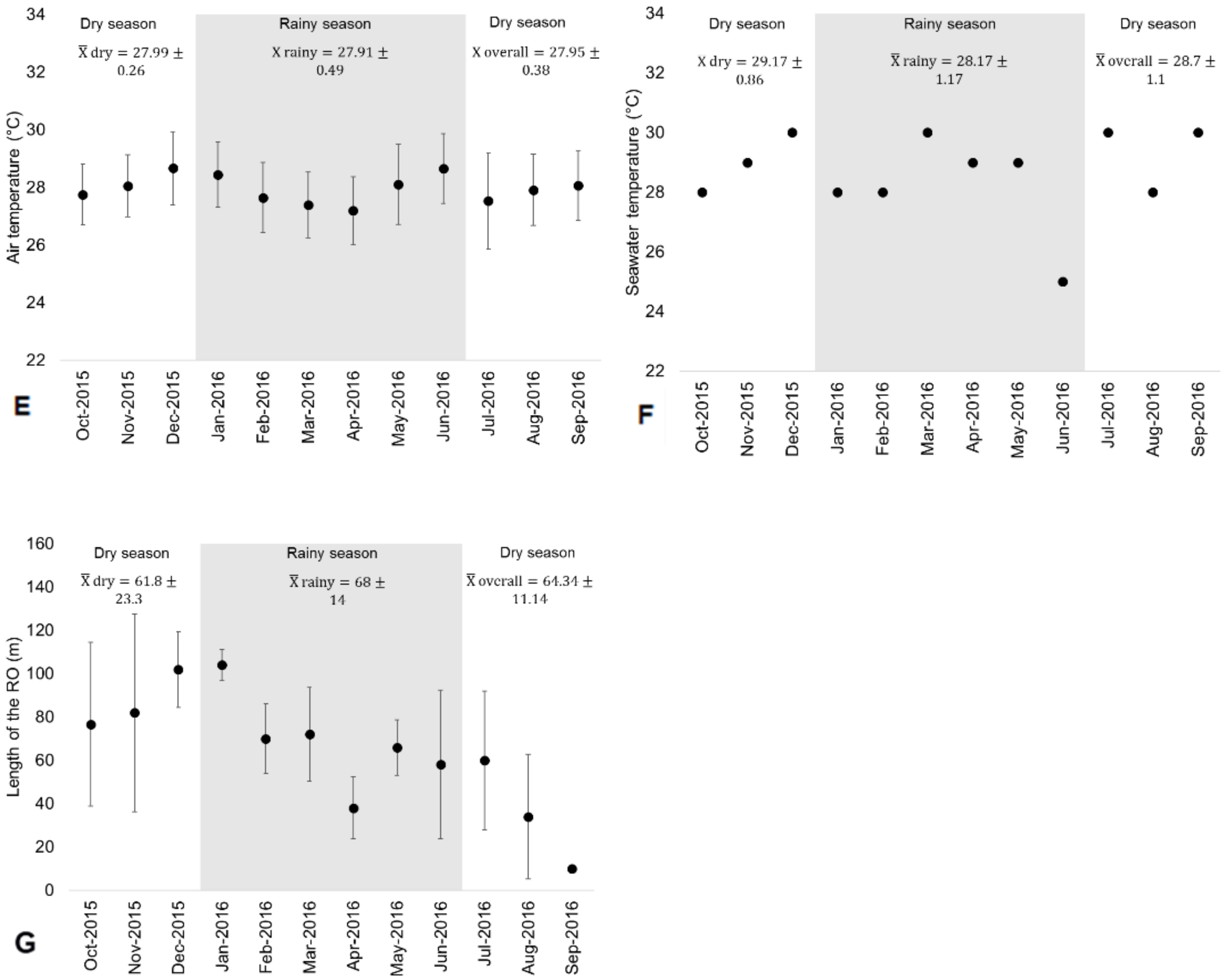

Fig. 2 (cont.). Physical factors and length of the range of occurrence of *Ocypode quadrata* sampled on Corvinas beach, Salinópolis, Brazil. (E) Air temperature. (F) Seawater temperature. (G) Length of the range of occurrence. Whiskers indicate standard deviation of the mean.

3.2. Abundance variation

A total of 690 *O. quadrata* burrows was found, with and overall mean of 0.58 ± 0.25 burrows.m^{-1}. Increase in burrow numbers started in December 2015, reaching the highest value in January 2016 (1.23 ± 0.46 burrows.m^{-1}). A drop occurred in February and March, followed by a new peak in April, from which on a gradual decrease on burrow abundance followed until the end of the study. Lowest abundance recorded was 0.14 ± 0.05 burrows.m^{-1} in August 2016. The nested ANOVA showed significant differences between seasons and the months within them. Regarding seasons, ($F_{(1, 46)}$=14.51, p<0.01), abundance was higher on the rainy (0.78 ± 0.24 burrows.m^{-1}) than on the dry season (0.37 ± 0.13 burrows.m^{-1}). According to Tukey's post-hoc test, differences among months were due to significant higher values in January and May 2016 than in August and September 2016 ($F_{(10, 46)}$=2.211, p=0.03) (Fig 3). Analysis of environmental factors showed burrow abundance was related to increasing precipitation and decreasing grain size (that is, increasing φ values) (Table 1). Air and seawater temperatures did not exert significant influence, whereas salinity and sediment sorting coefficient had high collinearity with precipitation and particle size, respectively, and were excluded from the multiple regression analysis.

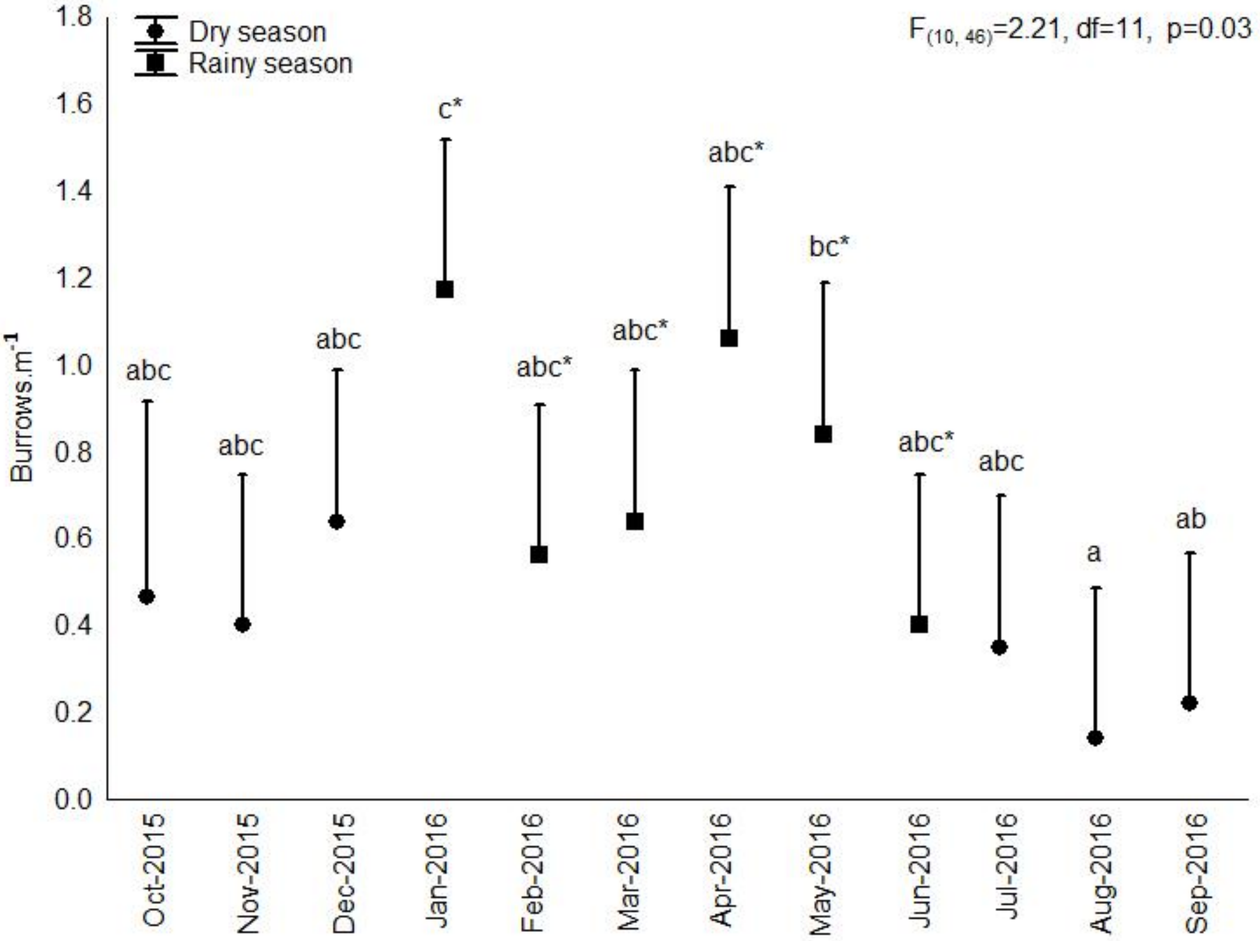

Fig. 2. Mean abundance and standard deviation of *Ocypode quadrata* burrows (burrows.m^{-1}) on Corvinas beach from October 2015 to September 2016. Asterisks (*) indicate significant higher overall abundance on the rainy season, comparatively to the dry season. Lowercase letters denote results of post-hoc Tukey test for abundance among months.

Table 1

Parameters estimated through a forward stepwise linear model selection, for burrow abundance (burrows.m^{-1}) in relation to physical factors.

R^2	Adjusted R^2	$F_{(2,8)}$	p	S.E. of estimate
0.67	0.59	8.27	0.01	0.21
	Significant effects of physical variables			
	B	**D.f.**	**t**	**p-level**
Intercept	-9.5		-3.35	0.01
Precipitation (mm)	0.12	10	3.71	<0.01
Particle size (φ)	7.52		3.48	0.01

Variables analyzed are precipitation (mm), particle size (φ), air temperature (ºC) and seawater temperature (ºC). Significant variables are described.

3.3. Burrow zonation

The range of occurrence of burrows always bordered the high tide mark, beginning at a distance of 3.3 ± 5.3 m landwards from it on the rainy season and 7.6 ± 2.1 m landwards on the dry season. Burrows presence extended above the high tide mark in a mean distance of 71.3 ± 6.8 m on the rainy season and 65.1 ± 12.5 m on the dry season. Burrows were concentrated closer to the water line on both seasons, occurring in high numbers on the first 10 m above the drift line (Fig 4). On the dry season a relatively higher number of burrows was observed towards the end of the range of occurrence (Fig 4). Burrows were found on the intertidal only in March and August 2016, summing 12 burrows (~2% of the total), seven of which were only up to 10 m seawards from the high tide mark. Across-shore burrow size stratification was not very pronounced on Corvinas beach, but still with some noticeable trends. Adult-sized burrows were present along the whole range of occurrence, while juvenile-sized burrows tended to concentrate at intermediate positions, specially on the dry season (Fig. 4). Juvenile-sized burrow frequency decreased farther than 90 m away from the high tide mark in both periods.

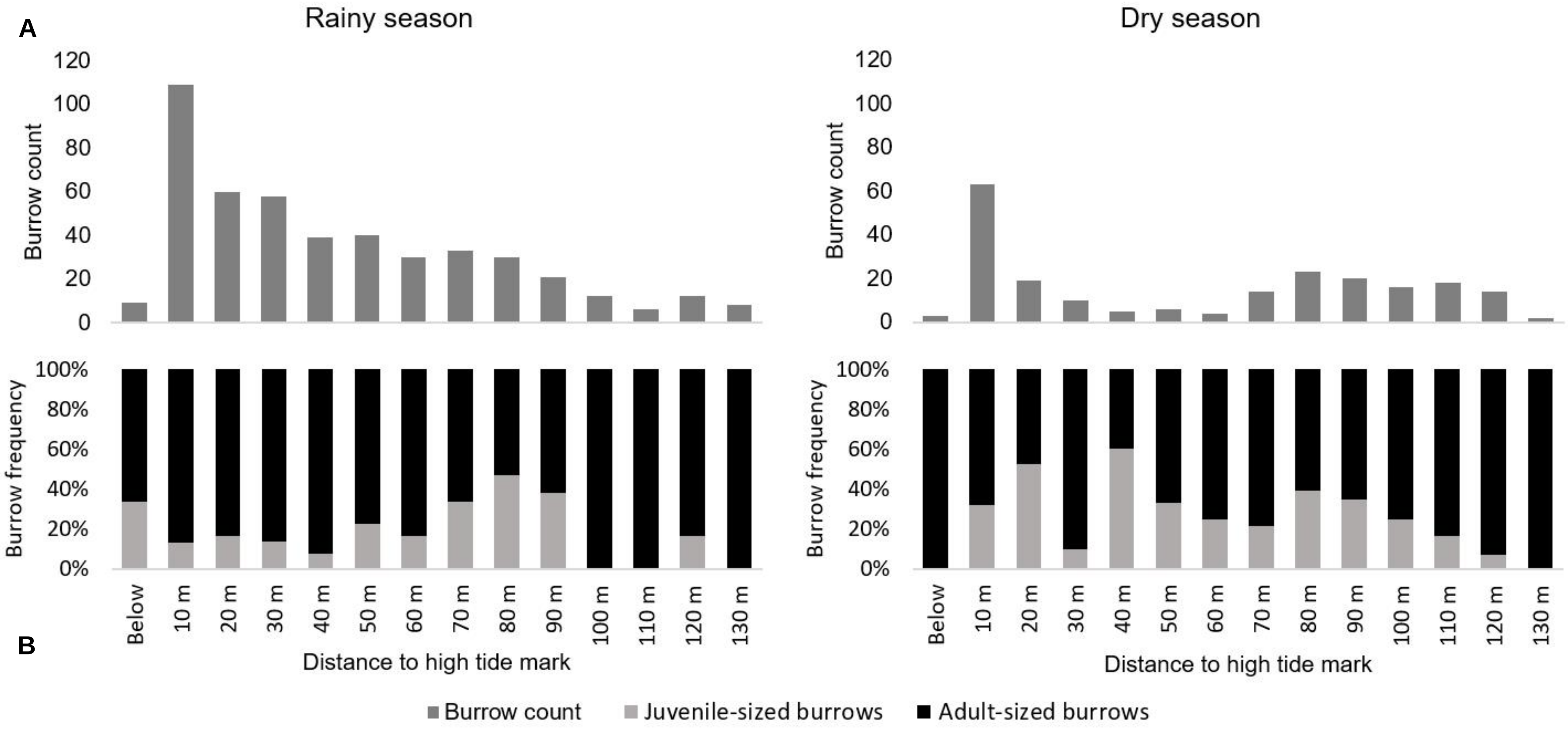

Fig. 3. *Ocypode quadrata* burrow distribution on Corvinas beach, Salinópolis, Brazil. Distribution of (A) *Ocypode quadrata* total burrow count and (B) frequency of adult (>20 mm burrow diameter) and juvenile-sized (<20 mm burrow diameter) burrows observed across the range of occurrence, regarding distance to the high tide mark, on both rainy and dry seasons at Corvinas beach.

3.4. Body growth

Values from the age-length key, obtained from modal progression analysis, allowed the estimate of the VBGM parameters L_∞, K, t_0, although the latter parameter was not significant (Table 2 and Fig 5A). The C and WP parameters were equal zero, meaning individual growth did not diminish throughout the year. The value of L_∞ for *O. quadrata* in Corvinas beach was 53.36 mm, with a K value of 0.76 yr^{-1} and a t_0 of 0.014 years (Table 2). The growth curve successfully matched the main identified cohorts (Fig 5B), obtained by the equation $Length_{(t)}=53.36\{1-e^{[-0.76*(t-0.014)]}\}$. The bimodal distributions during the first sampling months (October-January) suggest that at least two main cohorts were co-existing. In the following months, the unimodal distribution may be reflecting a superposition of these two cohorts (February to April 2016). In May the distribution was again bimodal, but from then on the amount of individuals decreased to a point that hinders such assumption. However, fewer individuals of larger classes (>40 mm) were found, while smaller classes were again observed (July to September 2016). Overall, smaller classes were present for 8 months on Corvinas beach.

Table 2

Estimated values of von Bertalanffy growth model (VBGM) parameters, adjusted for *Ocypode quadrata* burrows on Corvinas beach from October 2015 to September 2016.

	Estimate	SE	t value	Pr(>|t|)
L_∞ (mm)	53.36	2.58	20.65	3.78e-10
K (yr^{-1})	0.76	0.09	8.19	5.24e-06
t_0 (years)	0.014	0.05	0.3	0.77
Φ	3.34	-	-	-

Values are followed by its standard error (SE) when available.

* L∞ = asymptotic length. K = growth parameter. t_0 = theoretical point in time of zero length. Φ = growth performance index.

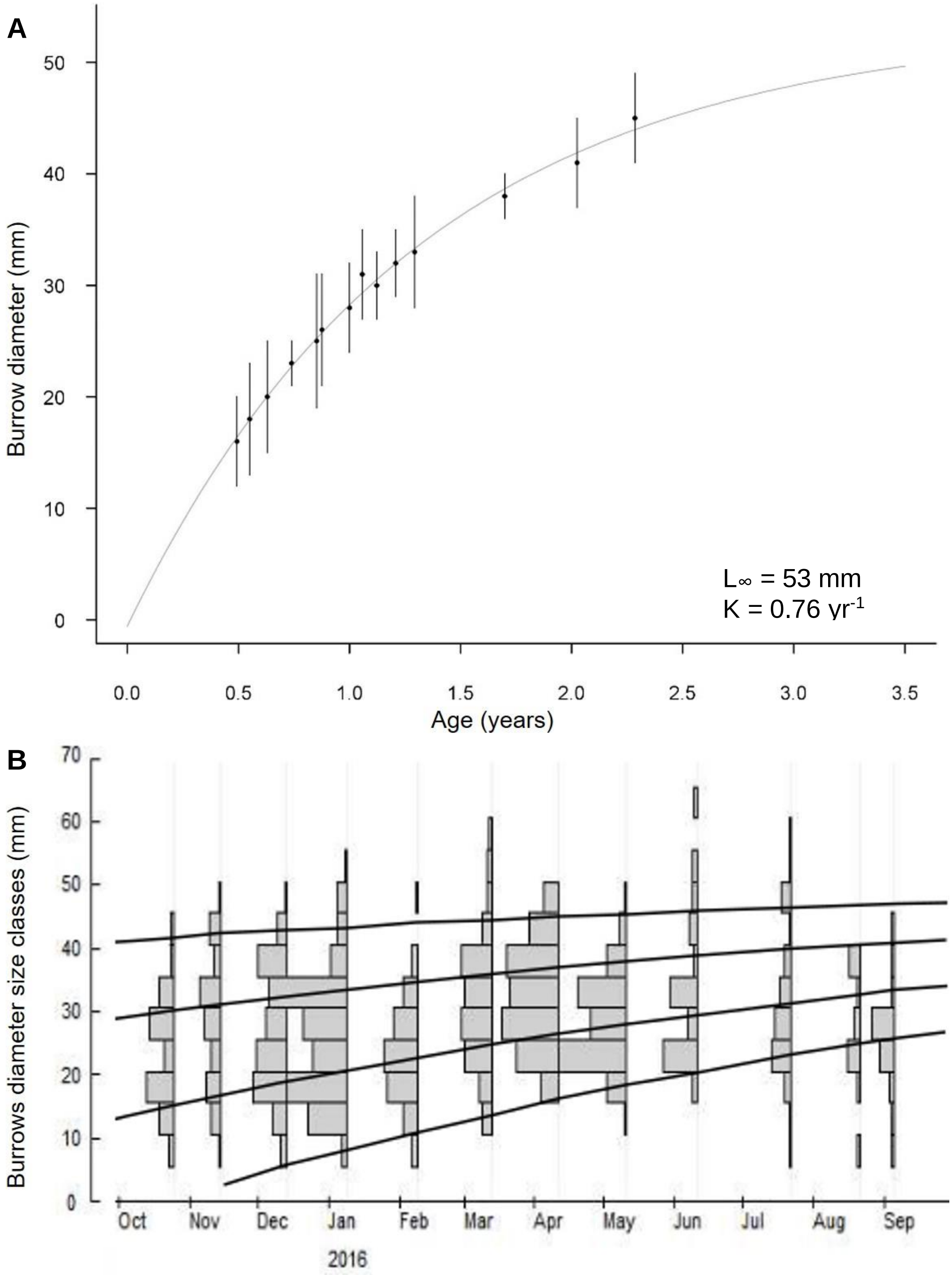

Fig. 4. Individual growth curve of *Ocypode quadrata* in Corvinas beach, Salinópolis, Brazil. (A) Growth curve with estimated parameters of asymptotic length (L∞) and growth constant (K). (B) Monthly frequency of size classes, with estimated growth curve following cohort progression.

3.5. Direct assessments

Of 213 excavated burrows on the three months of direct assessments, 42 burrows were occupied (19.72%). Occupation rate was higher on March 2016 (28.07%), and lower on September (18.1%) and June 2016 (12.5%) (Fig 6A). Most individuals were captured close to the high tide mark, and all up to 50 meters above with only two exceptions on June 2016 (Fig 6B). A total of 24 males and 16 females were collected. Only 2 juveniles were found, one at each season. The rainy season had a similar amount of females than males (11 versus 9), while the opposite took place in the dry season, with a greater difference (15 males against 5 females). This difference on sex ratio among seasons was significant ($x^2 = 5.45$, d.f. = 1, $p = 0.02$). Further, there was a significant difference from the expected 1:1 frequency between sexes, according to the chi-square test ($x^2 = 26.67$, d.f. = 1, $p < 0.01$), for a general proportion of 3:2 males to females. A single ovigerous female, 34 mm carapace width, was found throughout the study, on March 2016.

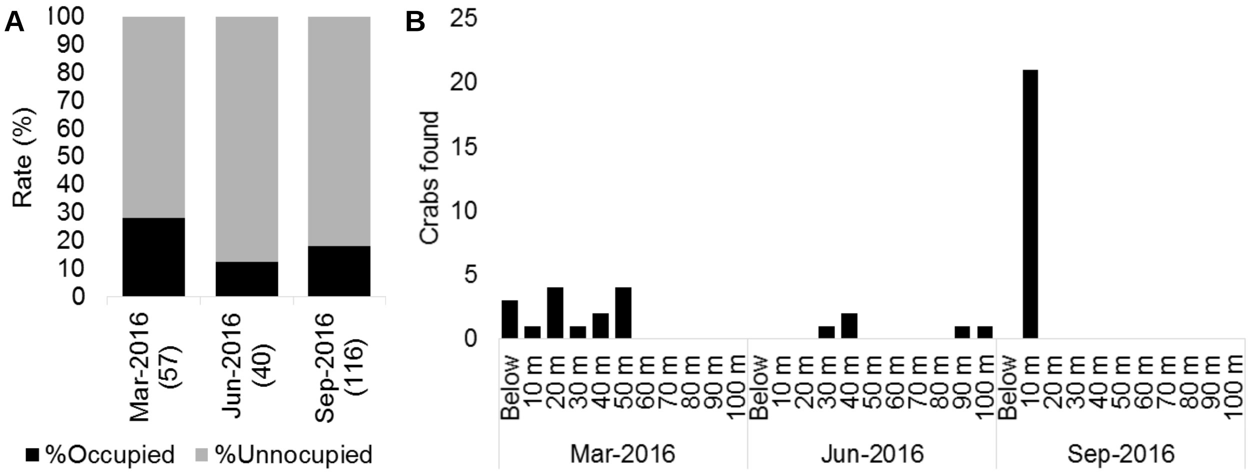

Fig. 5. Burrow occupation at Corvinas beach, Salinópolis, Brazil. (A) Burrows occupation rate per direct assessment event. Numbers in parentheses indicate total number of burrows excavated. (B) Burrow occupation regarding distance to the high tide mark, per direct assessment event.

Burrow diameter (BD) had a significant relationship with carapace width (CW) ($r^2 = 0.525$, $p < 0.01$, BD = 6.18 + 0.73(CW), Fig 7). It was also significant related to carapace length (CL) and height (CH), however with smaller regression coefficients: CL: $r^2 = 0.46$, $p < 0.01$, BD = 10.35 + 0.7307(CL); CH: $r^2 = 0.33$, $p < 0.01$, BD = 11.61 + 0.9148(CH). Minimum and maximum burrow diameters measured were 8.6 and 43 mm respectively, therefore with respective individuals estimated as 3.3 and 50.1 mm carapace width. Minimum and maximum carapace width measured were 8.3 and 47, with a mean of 32.28 ± 7.34 mm.

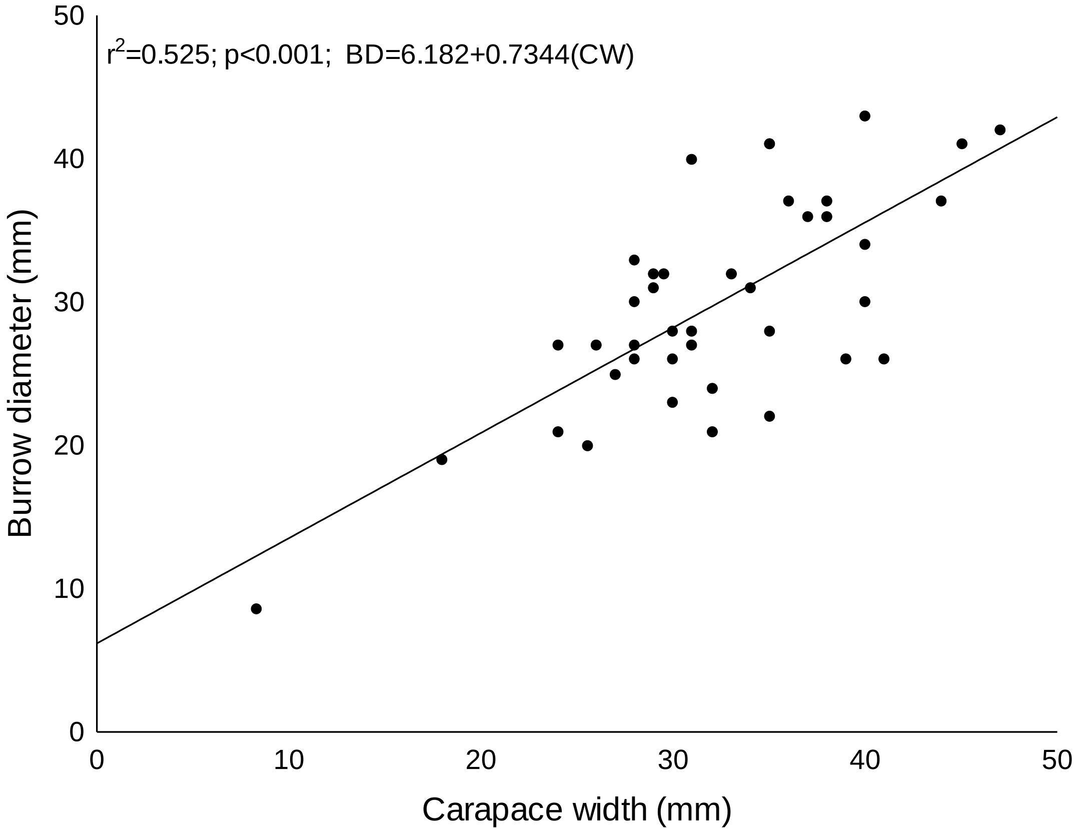

Fig. 6. Linear regression between *Ocypode quadrata* carapace width (CW) and burrow diameter (BD). Data was sampled on March, June and September 2016. *n* = 40 (outliers were excluded).

4. Discussion

Burrow abundance showed marked difference between the two seasons. Burrow numbers increased on rainy season and declined on following dry season months. The lower number of burrows sampled on the last months of this study may reflect natural mortality on the population. Since the population on Corvinas beach is mainly restricted to the supralittoral zone, drier months present a harsher environment prone to dehydration, contributing to crab mortality (Weinstein et al., 1994). Conversely, elevated rainfall during the rainy season may turn the environment more suitable for *O. quadrata*: rainy months on the Amazon region present increased tide heights, due mainly to larger riverine freshwater discharge (Geyer et al.,1996; Nittrouer and DeMaster, 1996). During this study, we observed the high tide mark migrate landwards, up to the drift line reaching the vegetated dunes in March and April. This phenomenon could result in easier seafood availability and a lower risk of dehydration inside the range of occurrence of *O. quadrata*. We also observed increasing vegetation growth on rainy months, with can function as shelter and offer food resources, such as insects (Branco et al., 2010; Lucrezi and Schlacher, 2014). The larger range of occurrence on the rainy season indicates broader areas with satisfactory conditions for *O. quadrata* presence. Rainfall relevance to the ghost crab population at this Amazon coast beach is also indicated by the strong positive relationship among burrow abundance and precipitation.

Sediment particle size was the only other variable with significant influence on abundance, even though sediment characteristics on Corvinas beach did not vary markedly over time. This factor is directly related to beach morphodynamics (Defeo and McLachlan, 2005; McLachlan and Brown, 2006; Defeo and McLachlan, 2011), hence is an important predictor for sandy beach macrofauna. Salinity was excluded from the model due to high collinearity, but can be a relevant factor due to a ghost crab tolerance range of 12 to 40 reported on the literature (Santos et al., 1989; Branco et al., 2010). It should exert more influence over ghost crab populations where broader salinity fluctuation occurs, while Corvinas beach stayed within the tolerance range on the studied period. Air temperature reportedly influences ghost crab populations in regions where it has broad variations (Milne and Milne, 1946; Haley, 1972; Negreiros-Fransozo et al., 2002; Branco et al., 2010). It is not a significant factor on Corvinas beach probably due to its stability, as a similar result was found on a 5 °C range in south Brazil (Neves and Bemvenuti, 2006). Latitudinally, no clear trends of *O. quadrata* abundance are noticeable (Table 3). This contrasts with trends of higher abundance towards subtropical regions reported for sandy beach crustaceans as *Emerita brasiliensis* and *Excirolana braziliensis* (Defeo and McLachlan, 2005). Density, however, seems to be lower on tropical regions than in higher latitudes (Table 3), similarly to the aforementioned trends. An attempted correlation between density and latitude did not find a significant effect (r=-0.4, p=0.35), possibly due to few data points.

The relationship between particle size and burrow abundance was of higher values towards finer sediments, as expected by the HHH. Similarly, Pombo et al. (2017) found a positive relation with density and particle size, with higher densities towards dissipative conditions. This trend emerges from the benefits of dissipative environments, where lesser harshness of physical factors lead to increased growth and reproduction of individuals (Defeo and McLachlan, 2005). However, Pombo et al. (2017) also found higher densities with steeper beach slopes, a condition found towards reflective conditions, similar to trends reported by Turra et al. (2005), Defeo & McLachlan (2011) and Lucrezi (2015). Steeper slopes can favor supralittoral populations by elevated beach backwards functioning as shelter from adverse conditions (Pombo, 2015; Pombo et al., 2017). While Corvinas beach is dissipative with low beach slope, our zonation pattern showed *O. quadrata* as a predominantly supralittoral population, with range of occurrence majorly above the latest tidal drift line, i. e. the high tide mark.

This supralittoral predominance on ghost crab distribution can be reasonably explained by Corvinas beach wide intertidal zone and *O. quadrata* behavioral aspects. This species feeds by non-predatory (deposit-feeding on patches of benthic diatoms and scavenging on items left by receding tides like carcasses, plant detritus and organic litter) (Milne and Milne, 1946; Robertson and Pfeiffer, 1981; Lucrezi and Schlacher, 2014) and predatory feeding habits (preying on smaller marine invertebrates, insects, hatchling turtles and several other organisms) (Fales, 1976; Wolcott, 1978; Branco et al., 2010; Lucrezi and Schlacher, 2014; Tewfik et al., 2016). These habits require venturing into the intertidal zone, towards damp sands and the water line, or the drier terrestrial area. *O. quadrata* is adapted to both, being highly mobile (Milne and Milne, 1946; Wolcott, 1978) and having tuffs of hydrophilic setae that are used in uptake of soil interstitial water (Wolcott, 1976, 1984). However, due to Corvinas beach wide intertidal zone, moving towards the water line would require a great energy expenditure while exposed to elevated tropical temperatures and higher risk of predation. Conversely, its supralittoral is sheltered by vegetated dunes. Food can be acquired on high tide drift lines and possibly as terrestrial organisms among the vegetation. The higher burrow numbers found towards the high tide mark suggests that the lower limit of the range of occurrence is more suitable, since food and water availability are greater, with dunes still providing reasonable resources. In light of our regression results and the spatial distribution of *O. quadrata* in Corvinas beach, we agree with those findings of Pombo et al. (2017).

It is important to highlight that *O quadrata* is still associated to the water during early stages of its life cycle. Juveniles have limited moving and burrowing capabilities and lower resistance to dehydration, often remaining within the intertidal and moving upwards as the crabs moult into subsequent phases, resulting in a size stratification pattern (Milne and Milne, 1946; Alberto and Fontoura, 1999; Turra et al., 2005; Branco et al., 2010; Pombo, 2015; Pombo et al., 2017). This pattern is not so much evident on Corvinas, since burrows rarely show on the intertidal. Juvenile burrows (<20 mm) are spread above the drift line, not reaching the uppermost limits of the range of occurrence. Adult-sized burrows are present throughout the whole range of occurrence, probably as their capabilities allows the colonization of farther distances. Adult sizes may also confer competitive advantages, allowing for occupation of resource-rich areas, such as the drift line immediacies. Hence, smaller burrows distribution might be driven by intraspecific competition and the moving limitations of juveniles.

The few studies that report *O. quadrata* individual growth parameters were performed at Brazilian southeastern coast (Pombo, 2015; Oliveira et al., 2016). Our L_∞ (asymptotic length) value is intermediate between the two available studies, and our K (growth constant) is equal to Oliveira et al. (2016) and lower than Pombo (2015) (Table 3). This resulted in an intermediate growth performance index, smaller than that of Oliveira et al. (2016) and higher than that of Pombo (2015) (Table 3). Population data for intertidal crustaceans, especially *Emerita* and *Excirolana* species (Cardoso and Defeo, 2003, 2004; Defeo and McLachlan, 2005, 2013), suggests an increasing growth and mortality rates towards the tropics. We did not calculate mortality rates due to possible biases arising from uncollapsed, abandoned burrows, mostly of larger sizes (Pombo, 2015). The intermediate growth parameters found at Corvinas beach, compared to southern regions, suggest that local, within-beach factors may account for spatial variability on *O quadrata* populations, overcoming latitudinal trends. This is also evidenced on the work of Pombo (2015), where individual growth parameters on three morphodynamically distinct beaches had greater variation than relatively to Oliveira et al. (2016) and this study (Table 3).

Latitudinal trends can be discerned for body size, however. Our maximum carapace width (47 mm) was larger than most published data at southern latitudes, while being smaller than north latitudes (up to 50 mm for Texas in Haley (1972), Table 3). This is interesting, since latitudinal trends found in other crustaceans suggests in decreasing body size towards tropical beaches (Defeo and Cardoso, 2004; Defeo and McLachlan, 2005, 2013). While data for *O. quadrata* shows increasing body size towards norther latitudes, it appear that it decreases on southern latitudes (Table 3).

Table 3

Different *Ocypode quadrata* population parameters reported along several latitudes, on undisturbed beaches.

Latitude	Tidal regime /Beach type	Individual growth parameters				Sizes	Abundance	Density (m^{-2})	Source
		L$_\infty$ (mm)	K (yr^{-1})	t$_0$ (yr)	Φ				
35°20' - 35°40' N	Microtidal, Reflective	NI				NDI	NI	0.04 bur/m^2	Hobbs et al., (2008)
27°40' N	NI	NI				53 mm	NI	NI	Haley, (1972)
18°39' 02" N	NI	NI				2 - 51 mm (BD)	NI[1]	0.49 - 1.79 bur/m^2	Valero-Pacheco et al., (2007)
0°36' 12.55" S	Macrotidal /Dissipative	53.36	0.76	0.014	3.34	8.6 - 43 mm (BD); 8.3 - 47 mm (CW)	0.58 ± 0.25 bur.m^{-1}	0.01 ± 0.01 bur/m^2	**This work**
7°51' - 8°45'30" S	Reflective to intermediate	NI				3.8 ± 54.7 mm (BD)	NI	0.1 - 0.3 bur/m^2	Souza et al., (2008)
22°57′ S	NI	58	0.73	-0.082	3.39[6]	4 - 40 mm (CW), 6 - 57 mm (BD)	83 ± 26.4 bur	0.046 - 0.675 bur/m^2	Oliveira et al., (2016)
23°21' 15" S	Microtidal to mesotidal/ Dissipative to reflective	46.36 (Dissipative) 57.95 (Intermediate) 53.01 (Reflective)	0.9 (Dissipative) 0.87 (Intermediate) 1.11 (Reflective)	-0.19 (Dissipative) -0.12 (Intermediate) -0.07 (Reflective)	3.29 (Dissipative) 3.46 (Intermediate) 3.49 (Reflective)	21.01 ± 7.75 mm (BD)		0.3 - 0.76 bur.m^{-2}; 0.3 - 0.37 ind.m^{-2}.	Pombo, (2015); Pombo et al., (2017)
23°23' 48" S	NI	NI				6.1 - 32 mm (CW)[2]	107.83 bur	NI	Corrêa et al., (2014)
23°27′ 36″ S	NI	NI				5.8 - 39.2 mm (CW)	48.4 ± 16.25 bur[3]	NI	Negreiros-Fransozo et al., (2002)
23°48' S	Microtidal /Reflective to intermediate	NI				NDI[4]	0.51 - 2.94 ind/m^2	NDI	Turra et al., (2005)
26°55' 56" S	NI	NI				4 - 38 mm (CW)	90.47 ± 85.82 bur	NI	Branco et al., (2010)

30° S	NI	NI	5.2 - 40.4 mm (BD); 5.2 - 34.4 mm (CW)	155 ± 48.4 bur[5]	NI	Alberto and Fontoura, (1999)]
30°05' 80" S	Microtidal /Dissipative	NI	NI	NI	0.4 - 5 $bur.m^{-2}$	Neves and Bemvenuti, (2006)

We favored parameters from dissipative states when several beach types were assessed. Since many results are in terms of density (burrows or individuals per m^2), we also calculated such value for the studied period on Corvinas Beach. *Tidal regime/Beach type refer to tidal and morphodynamic characteristics reported by each author. Growth parameters refer to asymptotic length (L_∞), growth constant (K), age at length 0 (t_0) and growth performance index (Φ). Sizes refer to the burrow diameter (BD) or carapace width (CW). Abundance and Density information was either given by the authors or an average value was estimated if possible. “bur” refers to raw number of burrows. **NI: Not Informed. ND: Not Detailed, applicable when data was used by the authors, however not in enough detail for precise estimation of average values for the study areas.

[1] Valero-Pacheco et al. (2007) sampled the entire beach, returning the exceptionally high abundance value (estimated in 106426 +- 43123.670 for the sampling period).

[2] The maximum 32 mm CW reported is a measure from the biggest ovigerous female. The authors did not inform maximum sizes for non-ovigerous females or males.

[3] Estimated as a mean of burrow abundance in 12 sampled months.

[4] Burrow diameter information is available only as mean histograms for different zones of the studied beaches, without ranges or overall estimates of size for each area. Maximum mean CW is approx. 30 mm.

[5] Abundance was averaged from the number of burrows reported from five separate sampling events, two in February 1991, one on March 1991, one on February 1993 and one on March 1993.

[6] The phi prime index was not reported by the author, but can be estimated using the other parameters.

Recruitment periods for *O. quadrata* have been both linked to warmer periods, even when reported as continuous throughout the year (Haley, 1972; Alberto and Fontoura, 1999; Negreiros-Fransozo et al., 2002; Branco et al., 2010; Pombo, 2015). Warmer, stable temperatures in tropical zones usually favors continuous recruitment (Costa and Negreiros-Fransozo, 1998; Negreiros-Fransozo et al., 2002). Still, we observed a bimodal distribution from October 2015 to January 2016, probably resulting from previous reproductive peaks. Smaller classes appeared from October 2015 to February 2016, and later from July to September 2016. This period coincides with recruitment peaks reported by Alberto and Fontoura (1999) (Jan-May), Negreiros-Fransozo et al. (2002) (Jan-Mar), Branco et al. (2010) (Jul, Feb, May), Pombo (2015) (Dec-Feb) and Oliveira et al. (2016) (Jun-Oct). Our absence of temperature effect over population abundance due to its stability on the tropical climate, suggests that temperature is not a recruitment-regulating factor on the Atlantic Amazon.

The importance of ghost crab burrow occupation rate has been appraised in recent studies (Pombo and Turra, 2013; Silva and Calado, 2013; Pombo et al., 2017). Its relevance consists in the possibility that abandoned burrows remain open due to environment characteristics, collapsing only after some time, lasting even weeks (Pombo et al. submitted). This may lead to biased estimations of population size because of habitat heterogeneity (e.g. sediment compaction, sheltered areas, morphodynamics, impact), resulting in misconceptions when comparing distinct areas. For instance, there exists the possibility of overestimation of different age groups due to differential across-shore occupation rates (i.e., within the same beach) (Pombo et al., 2017). Still, although variations on within-beach occupation rate may occur, it is not considered a determinant problem to body growth analyses based on size modal progression (Pombo, 2015; Oliveira et al., 2016). Our occupation rate (19.72%) is within a 20 – 40% range found on dissipative beaches from southeast Brazil by Pombo and Turra (2013). It is slightly higher than the 14.9 – 27% range reported in northeast Brazil by Silva and Calado (2013), although these authors did not inform about beach physical characteristics or statistical treatment used. Nevertheless, since a low number of crab individuals was directly assessed on Corvinas beach, following conclusions relying on this data should be considered with care.

We found significant overall difference between sexes, with a proportion of 3 males to 2 females. Although we tested with a small sample, there is at least two accounts on *O. quadrata* literature with a higher proportion of males. A 3:1 proportion was reported by Milne and Milne (1946) in New Jersey (United States) shores, and a 10:3 proportion, perhaps the highest in *O. quadrata* literature, by Valero-Pacheco et al. (2007) in Veracruz (Mexico). Both studies performed punctual samples, rather than yearlong observations. Male predominance may result from a greater difficulty to find ovigerous females, which can remain within their burrows and close their entrance (Negreiros-Fransozo et al., 2002; Lucrezi and Schlacher, 2014). This behavior impairs detection and sampling of such females by conventional means (sampling individuals outside the burrows). Excavating, as carried out in our study, is thus less prone to such biases. Further, sex ratio varied among seasons on Corvinas beach, with a higher proportion of females on the rainy season higher of males on the dry season. Similar observations were made in southeastern Brazil by Branco et al. (2010) (female predominance in August and May and of males in July) and Pombo et al. (2017) (female predominance in February and of males in August). They suggest that changes in sex predominance might result from elevated female mortality rates associated to recruitment peaks, since females are fragile and exposed during larval release. Additionally, other works made in preserved beaches found an approximate number of males and females (Negreiros-Fransozo et al., 2002; Turra et al., 2005).

5. Conclusions

Our work highlights how ghost crab populations on the Amazon coast are affected by the marked differences between the regional seasons. Environmental changes induced by the pronounced rainfall increase on the rainy season led to higher abundance of *O. quadrata*, as well as an expansion of the overall area with burrow occurrence on the beach, probably resulting from milder conditions for individual subsistence. The dissipative, macrotidal aspect of Corvinas beach also gave insight on zonation patterns of this species. While studies performed on microtidal beaches showed presence of burrows beginning on the intertidal zone, our study area contained burrows almost restrictedly on the supralittoral zone. This results possibly from a combination of physical characteristics of Corvinas beach as *O. quadrata* behavioral aspects. Further, these findings support previously described trends of *O. quadrata* variation regarding morphodynamics: while favored by finer sediments, typical of dissipative beaches, they are also benefited by steeper slopes (Pombo, 2015; Pombo et al., 2017). Therefore, both HHH and HHS predictions do not fully encompass ghost crab variation tendencies. Results from our body growth analysis showed that there are no clear pattern of latitudinal variation, when comparing our parameters to the few available studies, from Brazil’s southeastern coast. Latitudinal trends found in other crustaceans suggests increasing abundance while decreasing body size towards tropical beaches (Defeo and McLachlan, 2005, 2013). However, a trend of increasing size towards northern latitudes seems to take place, instead of tropical ones. Abundance still does not exhibit a clear latitudinal pattern, while density on the other hand, seems to decrease in tropical beaches. New studies, covering more of the latitudinal range, are required to validate these patterns, checking whether they are strengthened or weakened in light of more evidence. Similar research with other supratidal organisms can also shed light on existing trends on the supralittoral macrofauna.

6. Acknowledgements

We thank CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) and FAPESPA (Fundação Amazônia de Amparo a Estudos e Pesquisas) Foundations for a postgraduate studentship, through which fieldwork was possible. We are also grateful to the Laboratório de Oceanografia Biológica, Instituto de Geociências and Instituto de Ciências Biológicas at the Federal University of Pará, Brazil, where workplaces and learning environments were readily available.

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CONCLUSÕES GERAIS

Este trabalho é o primeiro a ilustrar como populações da espécie *Ocypode quadrata* da costa amazônica são afetas por suas diferenças sazonais. Mudanças ambientais ocasionadas pelo aumento da precipitação pluviométrica na estação chuvosa levaram à uma maior abundância de *O. quadrata*, além de aumentar a extensão sua área média de ocorrência das tocas. O aspecto dissipativo e de macromaré da praia das Corvinas permitiu conclusões também a respeito do padrão de zonação da espécie: enquanto trabalhos conduzidos em ambientes de micromaré mostram que a espécie ocupa estratos superiores das praias a partir do início da zona entremarés, nossa área de estudo conteve tocas praticamente restritas ao supralitoral.

Nossos resultados suportam tendências previamente descritas de *O. quadrata* segundo a morfodinâmica praial. Enquanto sua abundância seja favorecida pela maior predominância de sedimentos finos no substrato, característica típica de praias dissipativas, ela também é beneficiada por maiores inclinações da face praial (Pombo, 2015; Pombo et al., 2017). Dessa maneira, tanto as predições da Hipótese da Severidade Ambiental (HHH – Habitat Harshness Hyphothesis) (Defeo and Martínez, 2003) quanto da Hipótese da Segurança do Habitat (HHS – Hyphothesis of Habitat Safety) (Defeo and Gómez, 2005) não englobam totalemente tendências encontradas em populações naturais de *O. quadrata*.

Resultados da análise de crescimento corporal não mostram padrão claro de variação latitudinal do mesmo, quando comparados com os poucos estudos disponíveis na costa das Américas. Para outros crustáceos, estudos sugerem padrões latitudinais de maior abundância e menor tamanho corporal em regiões tropicais (Defeo and McLachlan, 2005, 2013). Para *O. quadrata*, porém, parece haver tendência de aumento de tamanho corporal em direção a latitudes ao norte. Não se observam tendências claras para abundância, enquanto a densidade populacional parece diminuir nos trópicos. Novos estudos, cobrindo mais da distribuição latitudinal da espécie, serão necessários para validar esses padrões, ajustando-os ou corrigindo-os sob a presença de mais dados. Do mesmo modo, novas pesquisas investigando populações e organismos da zona supralitoral podem trazer novos entendimentos sobre as tendências naturais da macrofauna nativa dessa zona.

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