



Population structure and reproductive biology of the fiddler crab *Leptuca leptodactyla* (Rathbun in Rankin, 1898) (Brachyura: Ocypodidae) in two estuaries from Sergipe state

Estrutura populacional e biologia reprodutiva do chama-maré *Leptuca leptodactyla* (Rathbun in Rankin, 1898) (Brachyura: Ocypodidae) em dois estuários do estado de Sergipe

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Leptuca leptodactyla is a broad-fronted species with a wide distribution and complex reproductive behavior. To evaluate possible local variations, the present study aimed to analyze the population structure of *L. leptodactyla* in two tropical estuaries located at the same latitude. Additionally, the effect of seasonality of environmental factors on reproductive activity in the species was evaluated. Individuals were sampled by randomly throwing a 30×30 cm square into each estuary 20 times. The number of hoods in the internal area of the square was recorded, and subsequently, the entire internal area was excavated to approximately 20 cm. All individuals were placed in plastic bags and taken to the UFS Carcinology Laboratory. In addition to abundance, each individual had the carapace width measured, in males, the size of the largest cheliped was also measured, and in females the abdomen width was measured. These measurements were used to compare the size of individuals between estuaries and to estimate morphological sexual maturity. Among the abiotic factors, differences were found in the organic matter and grain size of the substrate. The Vaza-Barris estuary had a greater abundance of females, embryonated females, hoods, and larger individuals than the Sergipe estuary. The difference in population structure may be related to the difference in food availability and the different levels of anthropogenic impact between estuaries.

Key words: seasonality, recruitment, hoods.

Leptuca leptodactyla é uma espécie de frente larga, ampla distribuição e comportamento reprodutivo complexo. Para avaliar possíveis variações locais, o presente estudo teve como objetivo analisar a estrutura populacional de *L. leptodactyla* em dois estuários tropicais localizados na mesma latitude. Adicionalmente, foi avaliado o efeito da sazonalidade de fatores ambientais na atividade reprodutiva da espécie. Os indivíduos foram amostrados lançando aleatoriamente um quadrado de 30×30 cm em cada estuário 20 vezes. Foi registrado o número de cúpulas na área interna do quadrado e posteriormente toda a área interna foi escavada até aproximadamente 20 cm. Todos os indivíduos foram acondicionados em sacos plásticos e encaminhados ao Laboratório de Carcinologia da UFS. Além da abundância, cada indivíduo teve a largura da carapaça medida, nos machos também foi medido o tamanho do maior quelípodo e nas fêmeas foi medida a largura do abdômen. Essas medidas foram utilizadas para comparar o tamanho dos indivíduos entre estuários e estimar a maturidade sexual morfológica. Dentre os fatores abióticos, foram encontradas diferenças na matéria orgânica e no tamanho do grão do substrato. O estuário Vaza-Barris apresentou maior abundância de fêmeas, fêmeas embrionárias, cúpulas e indivíduos maiores que o estuário de Sergipe. A diferença na estrutura populacional pode estar relacionada com a diferença na disponibilidade de alimentos e com os diferentes níveis de impacto antrópico entre os estuários.

Palavras-chave: sazonalidade, recrutamento, cúpulas.

1. INTRODUCTION

Different populations may present intraspecific variation according to the latitude they inhabit [1, 2]. However, population structure can also vary when analyzed on a small scale, especially in heterogeneous environments such as estuaries [3, 4]. Estuaries are hydrodynamic coastal environments that present temporal and spatial variation in biotic and abiotic processes [5].

Variations in this environment can affect the distribution and population structure of resident species, such as fiddler crabs [6, 7].

Fiddler crabs are detritivores that feed on the organic matter available in the substrate [7]. Food availability can affect individual growth and reproduction [8]. The growth and onset of sexual maturity in intertidal crabs may be related to temperature, salinity, humidity, photoperiod, sediment texture, quantity, and quality of food available [9]. The variation in these factors, with the exception of photoperiod, is influenced by the tidal cycle and rainfall in estuaries [10]. Furthermore, the tidal cycle and rainfall can influence the activity time of fiddler crabs at the surface [11, 12]. These factors, together with the intrinsic characteristics of each estuary, may contribute to intraspecific variations in the population structure and reproductive biology of the species.

Leptuca leptodactyla is a fiddler crab with a wide distribution found in the intertidal zone of mangroves, bays, and estuaries, from southern North America to southern Brazil [13]. The species plays an important structural and functional role in the habitat [14], acting as an ecosystem engineer through its detritivorous eating habit and construction/maintenance of its burrows [15, 16]. The species also exhibits complex reproductive behavior, in which males build hoods over their burrows, which has been associated with their reproductive success [17], in addition to being an indicator of their reproductive activity [18].

Although it is a common species with considerable ecological importance, little information is available in the literature. In the northeastern region of Brazil, we can highlight the work of Bezerra and Mathews-Cascon (2006) [19] who studied population structure in Ceará, Santos et al. (2015) [20] who examined behavior in Rio Grande do Norte, Hampton et al. (2014) [21] who evaluated the morphological variation along the Brazilian coast, covering the states of Maranhão, Ceará, Pernambuco and Bahia, and Araújo et al. (2022) [22] who evaluated population dynamics in Pernambuco. The scarcity of information about the species in the state of Sergipe was reported by Thurman et al. (2013) [13] in their review on the distribution of fiddler crabs in Brazil.

To help fill the information gap regarding the species and to investigate potential local variations, the present study aimed to evaluate the population structure and reproductive biology of *L. leptodactyla* in different estuaries in the Sergipe state.

2. MATERIAL AND METHODS

2.1 Study site

The study was carried out in the estuaries of the Sergipe River (10°56'44''S; 37°02'69''W) and Vaza-Barris River (11°08'07''S; 37°09'30''W), which are approximately 25 km from each other, both located in the municipality of Aracaju, Sergipe, Brazil. The estuaries are part of the humid coastal tropical climate, characterized by a dry period (August to March) and a rainy period (April to July) [23]. The Sergipe estuary, defined according to the average levels of tide penetration and the occurrence of mangroves, covers an extension of 44km from the confluence with the Jacareica River, in the upper estuary, to the mouth, between the cities of Aracaju and Barra dos Coqueiros [24]. This estuary has a higher level of anthropization, receiving industrial and domestic sewage daily [25]. The Vaza-Barris estuary is approximately 20km long, its tributaries are the Tejupeba Água Boa and Paruí Rivers on the right bank and the Santa Maria River on the left bank. [24]. Its vegetation consists of remnants of the Atlantic Forest Biome and associated ecosystems, such as mangroves and restingas [26, 27]. It is a tourist place under high real estate pressure due to the expansion of the cities [28]. Despite the growing urbanization around it, presents less deposition of human inputs [29].

2.2 Data sampling

Collections were carried out monthly from January to December 2013, on days without rain, during low spring tides (new moon or full moon). Collections were conducted on consecutive days, first the samples were taken in the Vaza-Barris estuary, and the same procedure was repeated for the Sergipe estuary on the following day.

In each estuary, monthly, the temperature (°C) of the air and the epibenthos was measured with a mercury thermometer and samples of the epibenthos were collected with a spatula for analysis of the percentage of organic matter (OM) and granulometry. Therefore, for each estuary, 12 samples were obtained for each abiotic variable, one by month. Precipitation data were provided by the Special Superintendence of Water Resources and the Environment (SERHMA). For the OM analysis, 10g of the epibenthos was separated, previously dried for 1 h (60°C), then subjected to a muffle for 1 hour at 550°C and subsequently weighed, with the OM content determined by the difference in weight, which was subsequently converted into a percentage [30]. Particle size analysis was carried out using the differential sieving technique for each sample, in which 100g of the desalted sample was dried in an oven at 60°C and subsequently sieved using a set of 13 sieves with the following mesh openings: 4000, 2800, 2000, 1400, 1000, 710, 500, 355, 250, 180, 125, 90, 63µm, arranged in descending order and shaken for 10 minutes to separate the granules, whose contents were weighed again, thus finding the average percentage of each fraction [31]. The SYSGRAN program was used with the Folk and Ward (1957) [32] formula to provide the average grain diameter.

Fiddler crabs were sampled using a 30×30 cm square, randomly released 20 times in each estuary. In the inner area of the square, the number of hoods was recorded and then the area was excavated to a depth of approximately 20 cm, or until no more individuals were found. All fiddler crabs were placed in labeled plastic bags and kept refrigerated until arrival at the Carcinology Laboratory at the Federal University of Sergipe, where they were kept frozen until analysis. The crabs were sexed based on the asymmetry of the chelipeds and morphology of the abdomen, and individuals whose sex could not be determined were classified as undifferentiated. The carapace width (CW) was measured for all individuals using a digital caliper (0.01 mm). For males, the length of the largest propodus (MCL) was measured, while for females, the width of the abdomen (AW) was also measured.

The similarity between air temperature, substrate temperature, OM, and granulometry composition of the substrate were evaluated separately between estuaries using an analysis of variance (factorial ANOVA), with estuary (Vaza-Barris and Sergipe) and the period (rainy and dry) were the fixed factors. When necessary, a Tukey post hoc test was used to evaluate the differences between factors.

The abundance of fiddler crabs was assessed both overall and by sexual category (male, female and undifferentiated) between estuaries using an analysis of variance (one-way ANOVA), followed by a Tukey post hoc test when necessary. The abundance of embryonated females and hoods was compared between estuaries and periods using factorial ANOVA. The fixed factors were estuaries with two levels (Vaza-Barris and Sergipe) and periods with two levels (rainy and dry), followed by a Tukey post hoc test when necessary. The relationship between the abundance of embryonated females and hoods was assessed using simple linear regression analysis ($\alpha=0.05$).

The sex ratio was estimated as the quotient between the number of males and the total number of individuals in our samples. Thus, sex ratio values greater or less than 0.5 indicate a bias towards males or females in the population, respectively. For the total population and in each sampling month in the estuaries, deviations from a 1:1 sex ratio were tested using a binomial test ($\alpha=0.05$) [33]. The size of the crabs was evaluated overall and separately by sex category (male and female) using an analysis of variance (one-way ANOVA), followed by a Tukey post hoc test when necessary. The statistical analyses cited above were performed using Statistica 7.0 (StatSoft) with 95% significance level.

To estimate the morphological sexual maturity (MSM), the crabs were grouped into age categories according to the relationship between CW and MCL for males and CW and AW for females. These morphometric variables were chosen based on previous studies, allowing for comparison. Next, K-means analysis was performed on the log-transformed data matrix (ln). This method was based on the predetermined establishment of groups, assigning crabs to one of the groups through an interactive process that minimizes variance within groups and maximizes variance between groups. Subsequently, using the classification result of K-means, a discriminant analysis (DA) was applied, allowing the refinement of the groups. The analyses cited above were made using the Past version 4.06b. After separating the age groups, each age category was divided into size classes (0.5 mm). The proportions of young and adults in each size class were calculated, the data obtained were adjusted to a logistic equation ($y = a/(1+be^{-cx})$), and the size where 50%

of the individuals were in the adult form (CW_{50}) was estimated using interpolation. This statistical methodology was based on the work of Sampedro et al. (1999) [34] and Corgos and Freire (2006) [35].

3. RESULTS

3.1 Abiotic factors

The descriptive statistics of the air and substrate temperatures are shown in Table 1. Air temperature did not show significant differences for the interaction between estuary and period (factorial ANOVA: $F=0.99$, $p=0.33$). Similarly, no significant differences were found in air temperature between estuaries (factorial ANOVA: $F=0.11$, $p=0.73$) or between periods (factorial ANOVA: $F=3.42$, $p=0.07$).

Substrate temperature showed no interaction between estuary and period (factorial ANOVA: $F=1.53$, $p=0.23$), nor was there a difference between estuaries (factorial ANOVA: $F=0.93$, $p=0.34$). However, a significant difference was found between periods, with higher values observed during the dry period (factorial ANOVA: $F=7.63$, $p=0.01$).

Table 1: Air and substrate temperatures for the Vaza-Barris and Sergipe estuaries. Min.- minimum; Max.- maximum; s.d.- standard deviation.

Estuary	Season	Temperature (°C)					
		Air			Ground		
		Min.	Max.	Mean±s.d.	Min.	Max.	Mean±s.d.
Vaza-Barris	Dry	26	33.3	30±2.10	29	35	33.4±2.12
	Rainy	26.5	29	27.8±1.14	29.3	31	29.7±0.88
Sergipe	Dry	25.5	31.8	29±1.84	29.5	36.8	33.1±2.43
	Rainy	27	30	28.3±1.25	29.5	34.3	31.7±2.27

Data regarding organic matter, grain size, and substrate components are presented in Table 2. OM did not demonstrate significant differences in the interaction between estuaries and season (factorial ANOVA: $F=1.50$, $p=0.22$), but it showed significant differences between estuaries, with higher values in Vaza-Barris (factorial ANOVA: $F=22.4$, $p=0.00$), and between period, with higher values in the dry period compared to the rainy period (factorial ANOVA: $F=11.7$, $p=0.00$).

In the granulometric analysis, the prevalence of sandy substrate was observed in both estuaries (Table 2). Grain size showed no significant interaction between estuary and period (factorial ANOVA: $F=0.59$, $p=0.44$) but showed a difference between estuaries, with the Vaza-Barris estuary having larger grain sizes than the Sergipe estuary (factorial ANOVA estuary: $F=17.6$, $p=0.00$). There was also no difference in grain size in relation to period (factorial ANOVA: $F=2.22$, $p=0.14$).

Table 2: Mean grain diameter (ϕ), average percentage of substrate components, and average percentage of organic matter (OM) for the dry and rainy periods in the Vaza-Barris (VB) and Sergipe (SE) estuaries. s.d. - standard deviation.

Estuary	Season	Φ mean±s.d.	%Gravel mean±s.d.	%Sand mean±s.d.	%Silt mean±s.d.	%Clay mean±s.d.	%OM mean±s.d.
VB	Dry	4.0±0.6	0.5±0.6	79.5±6.7	4.0±1.1	16.0±5.5	2.3±0.5
	Rainy	3.5±0.8	0.2±0.2	85.0±6.5	2.8±0.4	12.0±6.6	1.5±0.4
SE	Dry	2.8±0.7	0.3±0.3	88.4±6.6	1.4±0.9	9.9±6.6	1.3±0.2
	Rainy	2.6±0.6	0.3±0.1	92.3±4.0	0.9±0.05	6.5±4.1	1.0±0.2

3.2 Population structure

A total of 11,729 *L. leptodactyla* specimens were collected: 5,873 in the Vaza-Barris estuary and 5,858 in the Sergipe estuary (Table 3), with no significant difference in total abundance

between the estuaries (one-way ANOVA, $F=0.003$, $p=0.95$). All sexual categories were present year-round, except for embryonated females that were not recorded in the Vaza-Barris estuary in May and June and in the Sergipe estuary in May (Figure 1).

When comparing the abundance among sexual categories, it was observed that there was no difference in the abundance of males between estuaries (one-way ANOVA, $F=1.72$, $p=0.18$). On the other hand, females were more abundant in the Vaza-Barris estuary than in Sergipe (one-way ANOVA, $F=9.29$, $p=0.00$). Undifferentiated individuals were more abundant in the Sergipe estuary than in Vaza-Barris (one-way ANOVA, $F=11.9$, $p=0.00$).

Table 3: Abundance and size of males, females, embryonated females (EF) and undifferentiated (Un) of *Leptuca leptodactyla* in the Vaza-Barris and Sergipe estuaries. s.d. - standard deviation.

Estuary	Category	N	Mean size±s.d. (mm)	Maximum size (mm)	Minimum size (mm)
Vaza-Barris	Male	2128	6.84±1.53	9.85	3.06
	Female	2072	6.51±1.51	9.26	3.03
	EF	203	7.41±0.73	9.26	5.24
	Un	1470	2.03±0.56	3.36	1.01
	Total	5873			
Sergipe	Male	1935	6.45±1.68	10.28	2.75
	Female	1717	6.03±1.70	9.82	3.02
	EF	127	7.68±0.94	9.71	3.37
	Un	2079	2.01±0.53	3.46	1.03
	Total	5858			

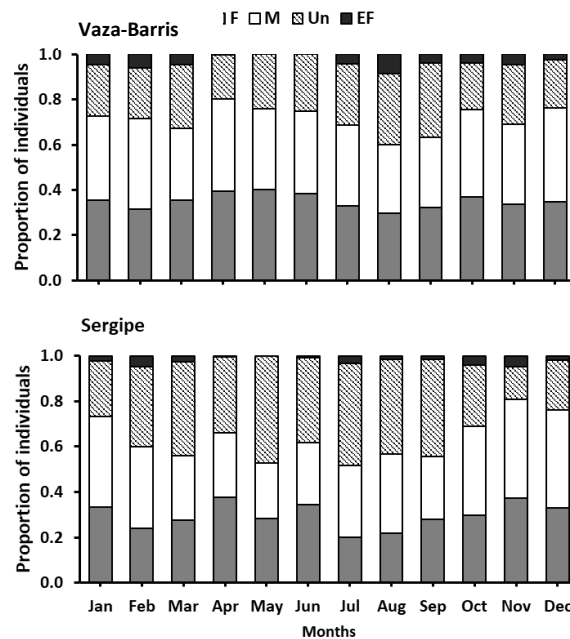


Figure 1: Monthly frequency distribution of the sexual categories of *Leptuca leptodactyla* in the Vaza-Barris and Sergipe estuaries. F, female; M, male; Un, undifferentiated; EF, embryonated female.

The abundance of embryonated females showed no significant interaction between estuary and period (factorial ANOVA: $F=3.77$, $p=0.05$). However, abundance was significantly higher in the Vaza-Barris estuary when compared to the Sergipe estuary (factorial ANOVA estuary: $F=4.26$, $p=0.04$), and also during the dry period (factorial ANOVA season: $F=35.4$, $p=0.00$).

Throughout the year, hoods were observed in both estuaries, with 255 recorded in the Vaza-Barris estuary and 154 in the Sergipe estuary. No hoods were recorded in April and May in the Vaza-Barris estuary, and in May in the Sergipe estuary (Figure 2). The abundance of hoods showed a significant interaction between estuary and period (factorial ANOVA: $F=5.42$, $p=0.02$).

Hoods were more abundant in Vaza-Barris estuary than in Sergipe estuary (factorial ANOVA estuary: $F=5.87$, $p=0.01$), with higher occurrence during the dry season than during the rainy season (factorial ANOVA season: $F=44.29$, $p=0.00$).

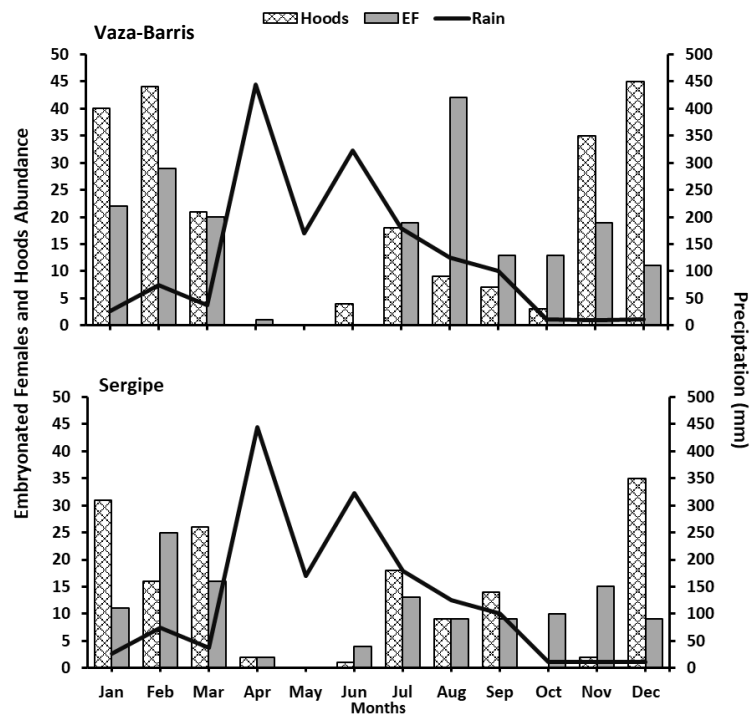


Figure 2: Abundance of embryonated females (EF) and hoods of *Leptuca leptodactyla*, and precipitation (mm) throughout the year in the Vaza-Barris and Sergipe estuaries.

Simple linear regression analysis revealed a significant influence between the abundance of embryonated females and the number of hoods in the Vaza-Barris estuary (Regression Analysis, $R^2:0.57$, $p=0.00$; Figure 3) and Sergipe estuary (Regression Analysis, $R^2:0.38$, $p=0.04$; Figure 3).

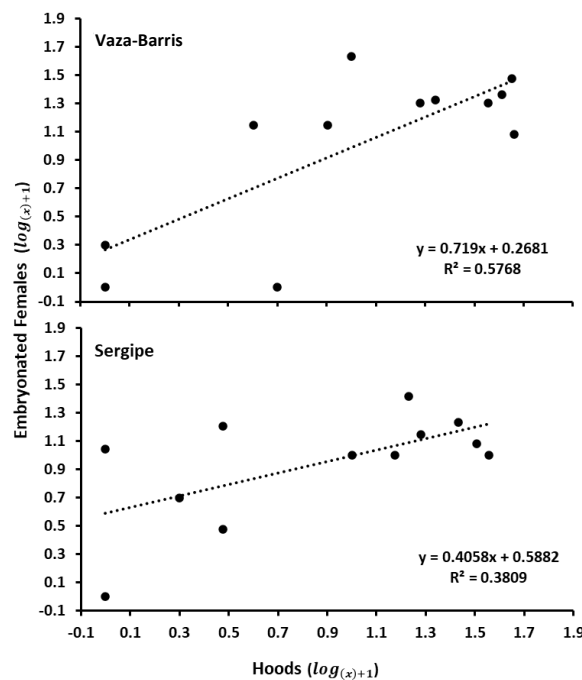


Figure 3: Simple linear regression analysis between the average number of hoods and embryonated females of *Leptuca leptodactyla* in the Vaza-Barris e Sergipe estuaries.

The sex ratio differed significantly from 1:1, with a female bias in the Vaza-Barris estuary (binomial test, $RS = 0.48$, $p=0.03$), but showed no significant difference in the Sergipe estuary (binomial test, $RS = 0.51$, $p = 0.14$). The sex ratio in the Vaza-Barris and Sergipe estuaries throughout the year is shown in Figure 4.

Males and females in the Vaza-Barris estuary were larger than those in the Sergipe estuary (one-way ANOVA, $F=60.4$, $p=0.00$; $F=83.6$, $p=0.00$ for males and females, respectively). The MSM was estimated for males and females at 5.82 and 5.55mm CW, respectively, in the Vaza-Barris estuary (Figure 5). In the Sergipe estuary, the MSM was 5.81 and 5.57mm CW for males and females, respectively (Figure 5).

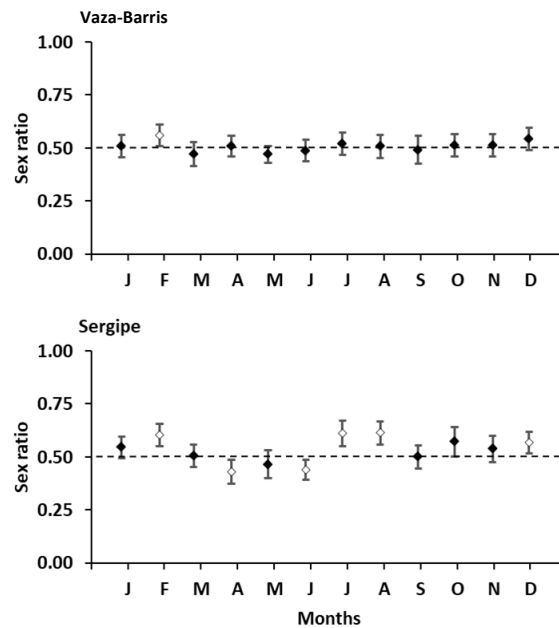


Figure 4: Sex ratio of *Leptuca leptodactyla* throughout the year in the Vaza-Barris and Sergipe estuaries. White diamonds indicate significant differences.

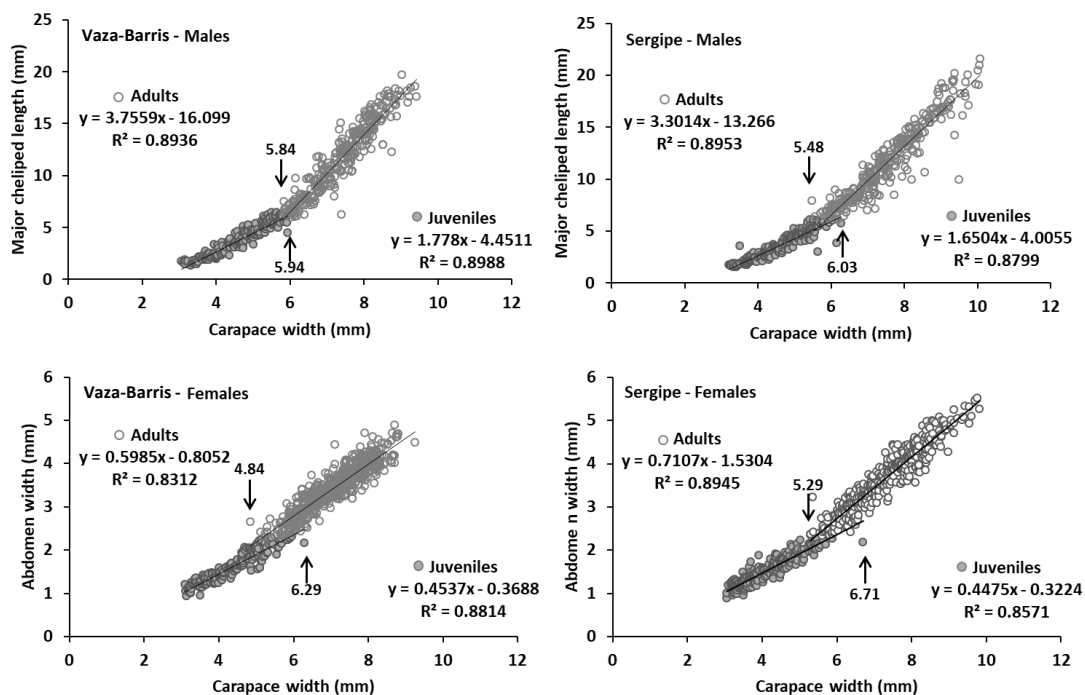


Figure 5: Regression between carapace width and major cheliped propodus of males and carapace width and abdomen width for females of *Leptuca leptodactyla* in the Vaza-Barris and Sergipe estuaries.

4. DISCUSSION

Leptuca leptodactyla exhibited differences in population structure even in estuaries located at the same latitude. Seasonal effects on reproduction were also observed in this species. Divergence between populations may be associated with local differences in each estuary. OM, the main food source for fiddler crabs [7, 36], was higher in the Vaza-Barris estuary compared to the Sergipe estuary, indicating differences in food availability.

The effective availability of food depends on ecosystem productivity, microbial activity, substrate texture, and tidal action [36]. In addition, local vegetation provides litter, which is an important source of organic matter for local primary production [37]. In the Vaza-Barris estuary, there is a lower rate of urbanization and anthropogenic impacts when compared to the Sergipe estuary, which may be associated with the higher local OM [38]. The vegetation on the banks of the Sergipe River estuary is degraded and urban expansion in the region has occurred since 1975 [39], which may be affecting the water circulation pattern and local productivity. Different factors can affect the distribution of fiddler crabs, including temperature, availability of organic matter and sediment grain size [7, 40]. Among these factors, only temperature did not show a significant difference among the estuaries studied.

Although the total abundance was similar between estuaries, the population structure showed divergence. The difference in female abundance between estuaries may be due to differences in survival rates. In *L. leptodactyla*, females leave their burrows and walk within the group to select the male for mating [41]. If they fail to find refuge when threatened, these females are prone to predation [42]. When threatened, fiddler crabs seek refuge in their burrows [43] and the presence of hoods can help in their location [44, 45]. In this sense, a lower occurrence of hoods was observed in the Sergipe estuary, which may have influenced the higher predation rate of females in this location.

Undifferentiated individuals were present throughout the year, indicating continuous recruitment in both estuaries. The higher recruitment in the Sergipe estuary may be associated with local structural features that promote greater larval retention in the studied area. The Sergipe Estuary presents a wide range of artificial substrates that were inserted to contain erosion caused by tidal incursion, which have altered water circulation and sediment deposition [46].

The greater abundance of embryonated females and hoods in the Vaza-Barris estuary may be related to the higher food availability in this estuary. In brachyurans, reproductive patterns result from a trade-off between growth and reproductive processes [47]. Male and female fiddler crabs allocate energy to reproduction in different ways [8]. In addition to producing gametes, males of *L. leptodactyla* build hoods over their burrows to attract females [45], change the color of their carapace [41] and exhibit waving behavior [48, 49]. Females, on the other hand, carry out ovarian and embryonic development [8] and move between the group of males to select the reproductive partner [50]. For these activities occur, there must be energy expenditure [8], which would justify the greater presence of reproductive activity in the Vaza-Barris estuary in the present work, as it presented greater availability of OM.

The higher frequency of embryonated females and hoods in the dry period in both estuaries indicates seasonality in the species reproductive activity, with a reproductive peak occurring in the dry period. The higher substrate temperature in the dry period may have contributed to greater reproductive activity. Temperature is one of the factors that influence the period of activity in fiddler crabs [18, 51]. The reproductive peak during the dry season was also observed in *Leptuca cumulanta* in a tropical estuary in northern Brazil [52]. Rainfall can also interfere with the period of crab activity on the surface [12]. Furthermore, increased precipitation during the rainy season can cause structural damage to burrows and hoods, negatively affecting the reproductive activity of *L. leptodactyla*.

In the present study, a positive relationship was observed between embryonated females and the presence of hoods. These hoods may serve as indicators of reproductive activity in *L. leptodactyla* [18]. In addition to attracting receptive females [17, 41], hoods have also been linked to territory demarcation [53], georeferencing [54], and improving thermal conditions inside the burrows [55, 56]. The low correlation between embryonated females and hoods may be related to the diversity of functions associated with hoods and various factors that influence reproduction in the species.

The sex ratio showed a deviation for females only in the Vaza-Barris estuary. This result may be related to the greater predation on males in this estuary. In fiddler crabs, the risk of predation is generally greater in males due to social behavior (waving) and sexual dimorphism (larger cheliped and lighter carapace), which make them more attractive to females, but also to predators [43, 57]. Greater engagement in reproductive behavior may have contributed to the higher predation rate of males in this estuary. It has been observed that males assess predation risk and are willing to take more risks when the probability of mating is greater [57]. It is worth mentioning that the Vaza-Barris estuary exhibited a greater occurrence of hoods, which indicates a higher reproductive investment for males in this location.

The larger size of individuals in Vaza-Barris is likely associated with the greater food supply in this estuary. The energy allocated for growth is influenced by the availability and quality of food, in addition to feeding frequency, which may vary according to location [36, 58]. On the other hand, the smaller size of *L. leptodactyla* individuals in the Sergipe estuary may also be related to the harmful effects that metals and other pollutants may have on crustaceans, which may cause interruption of molting and impairment of reproduction, among other effects [59, 60].

In the present study, males and females in both estuaries reached sexual maturity at smaller sizes than estimated in the Pacoti River, a tropical estuary located in Ceará, where *L. leptodactyla* individuals showed sexual maturity at 7mm [19]. In São Paulo, a subtropical region, the smallest size at sexual maturity was recorded in the Indaiá and Ubatumirim estuaries, where males of *L. leptodactyla* presented sexual maturity at 5.3 and 4.6 mm, respectively. While females showed sexual maturity in the Indaiá and Ubatumirim estuaries with 4.1 and 4.2mm, respectively [9]. In Santa Catarina, southern Brazil, the sexual maturity of males and females was estimated at 8.35 and 7.40mm, respectively [61].

In both estuaries, males reached sexual maturity at a larger size compared to females, which is possibly associated with the difference in energetic investment between the sexes, males tend to invest more in somatic growth, as size in males influences territory defense and reproductive success [62]. While females tend to invest more energy in gonadal and embryonic development [8].

5. CONCLUSION

Despite being located at the same latitude, *L. leptodactyla* populations exhibited intraspecific differences. Variations in recruitment, individual size, sex ratio, and reproductive activity were observed. These differences indicate plasticity of individuals according to the environment they inhabit and may occur due to factors intrinsic to estuaries, such as the dynamics of OM supply, ecological interactions and, especially, the level of anthropogenic impact. Small-scale studies are important to better understand the distribution of species, especially in the intertidal regions, where it is possible to observe zones with different abiotic and biotic characteristics. Although reproduction of fiddler crabs is generally continuous in tropical estuaries, an effect of seasonality on reproduction in the species was observed in both estuaries studied. A higher abundance of embryonated females and hoods was observed during the dry period, whereas in some months of the rainy period no evidence of reproductive activity was found. Thus, *L. leptodactyla* in the Vaza-Barris and Sergipe estuaries exhibits continuous reproduction with a reproductive peak in the dry period.

6. ACKNOWLEDGEMENTS

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7. REFERENCES

- Hines AH. Geographic variation in size at maturity in brachyuran crabs. *Bull Mar Sci.* 1989;45(2):356-68.
- Hopkins MJ, Thurman CL. The geographic structure of morphological variation in eight species of fiddler crabs (Ocypodidae: Genus *Uca*) from the eastern United States and Mexico. *Biol J Linn Soc.* 2010;100(1):248-70. doi: 10.1111/j.1095-8312.2010.01402.x
- Mokhtari M, Ghaffar MA, Usup G, Cob ZC. Determination of key environmental factors responsible for distribution patterns of fiddler crabs in a tropical mangrove ecosystem. *PLoS One.* 2015;10(1):1-17. doi: 10.1371/journal.pone.0117467
- Checon HH, Costa TM. The importance of considering small-scale variability in macrobenthic distribution: spatial segregation between two fiddler crab species (Genus *Leptuca*) (Decapoda, Ocypodidae). *Iheringia Série Zool.* 2018;108:1-8. doi: 10.1590/1678-4766e2018034
- Santos AKD, Oliveira ALL, Furtado JA, Ferreira FS, Araújo BDO, Corrêa JJM, et al. Spatial and seasonal variation of microphytoplankton community and the correlation with environmental parameters in a hypereutrophic tropical estuary - Maranhão - Brazil. *Brazilian J Oceanogr.* 2017 Jul;65(3):356-72. doi: 10.1590/s1679-87592017134406503
- Colpo KD, Negreiros-Fransozo ML. Comparison of the population structure of the fiddler crab *Uca vocator* (Herbst, 1804) from three subtropical mangrove forests. *Sci Mar.* 2004;68(1):139-46. doi: 10.3989/scimar.2004.68n1139
- De Grande FR, Granado P, Sanches FHC, Costa TM. Organic matter affects fiddler crab distribution? Results from field and laboratorial trials. *Estuar Coast Shelf Sci.* 2018 Nov;212:138-45. doi: 10.1016/j.ecss.2018.07.005
- Colpo KD, López-Greco LS. Dynamics of energy reserves and the cost of reproduction in female and male fiddler crabs. *Zoology.* 2018 Jan;126:11-9. doi:10.1016/j.zool.2018.01.004
- Cardoso RCF, Negreiros-Fransozo ML. A comparison of the allometric growth in *Uca leptodactyla* (Crustacea: Brachyura: Ocypodidae) from two subtropical estuaries. *J Mar Biol Assoc United Kingdom.* 2004;84(4):733-5. doi: 10.1017/S0025315404009828h
- Lacerda CHF, Barletta M, Dantas DV. Temporal patterns in the intertidal faunal community at the mouth of a tropical estuary. *J Fish Biol.* 2014;85(5):1571-602. doi: 10.1111/jfb.12518
- Christy JH. Pillar function in the fiddler crab *Uca beebei* (II): Competitive courtship signaling. *Ethology.* 1988;78(2):113-28. doi: 10.1111/j.1439-0310.1988.tb00223.x
- Wolfrath B. Observations on the behaviour of the European fiddler crab *Uca tangeri*. *Mar Ecol Prog Ser.* 1993;100(1-2):111-8. doi: 10.3354/meps100111
- Thurman CL, Faria SC, McNamara JC. The distribution of fiddler crabs (*Uca*) along the coast of Brazil: Implications for biogeography of the western Atlantic Ocean. *Mar Biodivers Rec.* 2013;6:1-21. doi: 10.1017/S1755267212000942
- Nobbs M. Effects of vegetation differ among three species of fiddler crabs (*Uca* spp.). *J Exp Mar Bio Ecol.* 2003;284(1-2):41-50. doi: 10.1016/S0022-0981(02)00488-4
- Jones CG, Lawton JH, Shachak M. Organisms as Ecosystem Engineers. *Oikos.* 1994;69(3):373-86. doi: 10.2307/3545850
- Kristensen E. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *J Sea Res.* 2008;59(1-2):30-43. doi: 10.1016/j.seares.2007.05.004
- Kim TW, Christy JH, Choe JC. Semidome building as sexual signaling in the fiddler crab *Uca Lactea* (Brachyura: Ocypodidae). *J Crustac Biol.* 2004;24(4):673-9. doi: 10.1651/c-2471
- Masunari S. Hood construction as an indication of the breeding period of the fiddler crab *Uca (Leptuca) leptodactyla* Rathbun, 1898 (Decapoda, Ocypodidae) from Guaratuba Bay, southern Brazil. *Crustaceana.* 2012;85(10):1153-69. doi: 10.1163/156854012X651277
- Bezerra LA, Mathews-Cascon H. Population structure of the fiddler crab "*Uca leptodactyla*" Rathbun, 1898 (Brachyura: Ocypodidae) in a Tropical Mangrove of Northeast Brazil. *Thalass An Int J Mar Sci.* 2006;22(1):65-74.
- Santos LC, Alencar CERD, Freire FAM, Luchiari AC. Agonistic interactions in the male fiddler crab *Uca leptodactyla* Rathbun, 1898 at varying densities. *Crustaceana.* 2015;88(6):625-40. doi: 10.1163/15685403-00003443
- Hampton KR, Hopkins MJ, McNamara JC, Thurman CL. Intraspecific variation in carapace morphology among fiddler crabs (Genus *Uca*) from the Atlantic coast of Brazil. *Aquat Biol.* 2014 Jan 13;20(1):53-67. doi: 10.3354/ab00545
- Araújo MSLC, Silva JVCL, Azevedo DS, Lima ML, Castiglioni DS. Comparative population dynamics of fiddler crab species (Crustacea, Ocypodidae) in two mangrove areas in northeast brazilian coast. *Nat Conserv.* 2022;15(3):46-62. doi: 10.6008/CBPC2318-2881.2022.003.0004

23. Souza MRR, Santos E, Suzarte JS, do Carmo LO, Soares LS, Santos LGGV, et al. The impact of anthropogenic activity at the tropical Sergipe-Poxim estuarine system, Northeast Brazil: Fecal indicators. *Mar Pollut Bull.* 2020 May;154:111067. doi: 10.1016/j.marpolbul.2020.111067
24. Carvalho MES, Fontes AL. A carcinicultura no espaço litorâneo sergipano*. *Rev da Fapese.* 2007;3(1):87-112.
25. Alves JPH, Passos EA, Garcia CAB. Metals and acid volatile sulfide in sediment cores from the Sergipe River Estuary, Northeast, Brazil. *J Braz Chem Soc.* 2007;18(4):748-58. doi: 10.1590/S0103-50532007000400013
26. Vasco AN, Mello-Junior AV, Santos ACAS, Ribeiro DO, Tavares ED, Nogueira LC. Qualidade da água que entra no estuário do rio Vaza Barris pelo principal fluxo de contaminação de água doce. *Sci Plena.* 2010;6(9):1-10.
27. de Oliveira J, Andrade EJ, Melo e Souza R, Costa DFS. Bioconcentração de metais (Cu, Fe, Zn, Mn e Pb) em *Crassostrea brasiliana* (Lamarck, 1819) nativa do manguezal do rio Vaza-Barris, Sergipe, Brasil. *Front J Soc Technol Environ Sci.* 2022 Aug;11(2):183-99. doi: 10.21664/2238-8869.2022v11i2.p183-199
28. Schwarz Junior R, Franco ACNP, Ribeiro AS, Martins MA, Soeth M, Cardoso OR, et al. Ecological and growth patterns of the longsnout seahorse *Hippocampus reidi* inferred by mark-recapture techniques in a tropical estuary. *Biota Neotrop.* 2021;21(2):1-9. doi: 10.1590/1676-0611-BN-2020-1130
29. Barbosa JCS, Santos LGGV, Sant'Anna MVS, Souza MRR, Damasceno FC, Alexandre MR. Seasonal distribution of aliphatic hydrocarbons in the Vaza Barris Estuarine System, Sergipe, Brazil. *Mar Pollut Bull.* 2016 Mar;104(1-2):343-6. doi: 10.1016/j.marpolbul.2016.01.037
30. Mantelatto LFM, Fransozo A. Reproductive biology and moulting cycle of the crab *Callinectes ornatus* (Decapoda, Portunidae) from the Ubatuva Region, São Paulo, Brazil. *Crustaceana.* 1999;72(1):63-76.
31. Wentworth CK. A scale of grade and class terms for clastic sediments. *J Geol.* 1922;30(5):377-92. doi: 10.1086/622910
32. Folk RL, Ward W. Brazos river bar: a study in the significance of grain size parameters. *J Sediment Petrol.* 1957;27(1):3-26. doi: 10.1306/74D70646-2B21-11D7-8648000102C1865D
33. Wilson K, Hardy ICW. Statistical analysis of sex ratios: an introduction. *Sex ratios: concepts and research methods.* 2002:48-92. doi: 10.1017/cbo9780511542053.004
34. Sampedro MP, González-Gurriarán E, Freire J, Muiño R. Morphometry and sexual maturity in the spider crab *Maja squinado* (Decapoda: Majidae) in Galicia, Spain. *J Crustac Biol.* 1999;19(3):578-92. doi: 10.2307/1549263
35. Corgos A, Freire J. Morphometric and gonad maturity in the spider crab *Maja brachydactyla*: a comparison of methods for estimating size at maturity in species with determinate growth. *ICES J Mar Sci.* 2006;63:851-9. doi: 10.1016/j.icesjms.2006.03.003
36. Saher NU, Qureshi NA. Food and feeding ecology of fiddler crabs species found along the coast of Pakistan. *Rom J Biol - Zool.* 2014;59(1):35-46.
37. Kristensen E, Bouillon S, Dittmar T, Marchand C. Organic carbon dynamics in mangrove ecosystems: A review. *Aquatic Botany.* 2008;89:201-19. doi: 10.1016/j.aquabot.2007.12.005
38. Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR. The value of estuarine and coastal ecosystem services. *Ecol Monogr.* 2011;81(2):169-93. doi: 10.1890/10-1510.1
39. Araujo HMP, Nascimento-Vieira DA, Neumann-Leitão S, Schwaborn R, Lucas APO, Alves JPH. Zooplankton community dynamics in relation to the seasonal cycle and nutrient inputs in an urban tropical estuary in Brazil. *Brazilian J Biol.* 2008;68(4):751-62. doi: 10.1590/S1519-69842008000400009
40. Casariego AM, Alberti J, Luppi T, Daleo P, Iribarne O. Habitat shifts and spatial distribution of the intertidal crab *Neohelice (Chasmagnathus) granulata* Dana. *J Sea Res.* 2011 Aug;66(2):87-94. doi: 10.1016/j.seares.2011.05.001
41. Rodrigues RO, Costa TM, Barreto RE. Burrow ornamentation in the fiddler crab (*Uca leptodactyla*): female mate choice and male-male competition. *Mar Freshw Behav Physiol.* 2016;49(5):317-25. doi: 10.1080/10236244.2016.1223784
42. Koga T, Backwell PRY, Jennions MD, Christy JH. Elevated predation risk changes mating behaviour and courtship in a fiddler crab. *Proc R Soc B Biol Sci.* 1998;265(1404):1385-90. doi: 10.1098/rspb.1998.0446
43. Takeshita F, Nishiumi N. Social behaviors elevate predation risk in fiddler crabs: quantitative evidence from field observations. *Behav Ecol Sociobiol.* 2022;76:162. doi: 10.1007/s00265-022-03268-5
44. Perez DM, Christy JH, Backwell PRY. Choosing a mate in a high predation environment: Female preference in the fiddler crab *Uca terpsichores*. *Ecol Evol.* 2016;6(20):7443-50. doi: 10.1002/ece3.2510
45. Pardo JCF, Stefanelli-Silva G, Christy JH, Costa TM. Fiddler crabs and their above-ground sedimentary structures: a review. *J Ethol.* 2020;38(2):137-54. doi: 10.1007/s10164-020-00647-1

46. da Silva RC. Nós vamos invadir sua praia: sobre a relação entre urbanização, turismo e erosão costeira no Brasil. *Brazilian J Dev.* 2022 Dec;8(12):78243-76. doi: 10.34117/bjdv8n12-098
47. Litulo C. Population structure and reproductive biology of the fiddler crab *Uca inversa* (Hoffman, 1874) (Brachyura: Ocypodidae). *Acta Oecologica.* 2005 May;27(3):135-41. doi: 10.1016/j.actao.2004.11.002
48. Rorato AC, Araujo SBL, Perez DM, Pie MR. Social cues affect synchronization of male waving displays in a fiddler crab (Crustacea: Ocypodidae). *Anim Behav.* 2017;126(April):293-300. doi: 10.1016/j.anbehav.2017.02.014
49. Backwell PRY. Synchronous waving in fiddler crabs: A review. *Current Zoology.* 2018;65(1):83-8. doi: 10.1093/cz/zoy053
50. Booksmythe I, Detto T, Backwell PRY. Female fiddler crabs settle for less: the travel costs of mate choice. *Anim Behav.* 2008 Dec;76(6):1775-81. doi: 10.1016/j.anbehav.2008.07.022
51. Colpo KD, López-Greco LS. Temperature influences the reproduction of fiddler crabs at the southern edge of their distribution. *Invertebr Biol.* 2017;136(2):171-83. doi: 10.1111/ivb.12168
52. Koch V, Wolff M, Diele K. Comparative population dynamics of four fiddler crabs (Ocypodidae, Genus *Uca*) from a North Brazilian mangrove ecosystem. *Mar Ecol Prog Ser.* 2005;291:177-88. doi: 10.3354/meps291177
53. Zucker N. Shelter building as a means of reducing territory size in the fiddler crab, *Uca terpsichores* (Crustacea: Ocypodidae). *Am Midl Nat.* 1974;91(1):224-36. doi: 10.2307/2424524
54. Christy JH. Predation and reproductive behavior of fiddler crabs (Genus *Uca*). *Evol Ecol Soc Sex Syst.* 2007;15(1):211-31. doi: 10.1093/acprof:oso/9780195179927.003.0010
55. Matthews LH. LXVI.— Notes on the fiddler-crab, *Uca leptodactyla*, Rathbun. *Ann Mag Nat Hist.* 1930;5(30):659-63. doi: 10.1080/00222933008673178
56. Powers LW, Cole JF. Temperature variation in fiddler crab microhabitats. *J Exp Mar Bio Ecol.* 1976;21(2):141-57. doi: 10.1016/0022-0981(76)90035-6
57. Koga T, Backwell PRY, Christy JH, Murai M, Kasuya E. Male-biased predation of a fiddler crab. *Anim Behav.* 2001;62(2):201-7. doi: 10.1006/anbe.2001.1740
58. Llodra ER. Fecundity and life-history strategies in marine invertebrates. *Adv Mar Biol.* 2002;87-170. doi: 10.1016/s0065-2881(02)43004-0
59. Bergey LL, Weis JS. Aspects of population ecology in two populations of fiddler crabs, *Uca pugnax*. *Mar Biol.* 2008 May;154(3):435-42. doi: 10.1007/s00227-008-0935-x
60. Barros MSF, Calado TCS, Santanna JL, dos Santos EV, Silva AS. Species composition and diversity of decapod crustaceans. *Biodiversidade.* 2020;19(2):82-96.
61. Masunari S, Swiech-Ayoub BP. Crescimento relativo em *Uca leptodactyla* Rathbun (Crustacea, Decapoda, Ocypodidae). *Rev Bras Zool.* 2003;20(3):487-91. doi: 10.1590/S0101-81752003000300020
62. Allen BJ, Levinton JS. Sexual selection and the physiological consequences of habitat choice by a fiddler crab. *Oecologia.* 2014;176(1):25-34. doi: 10.1007/s00442-014-3002-y