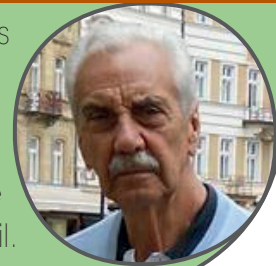




e-ISSN 2358-2936
www.scielo.br/nau
www.crustacea.org.br

This article is part of the special series offered by the Brazilian Crustacean Society in honor to **Nilton José Hebling** in recognition of his dedication and contributions to the development of carcinology in Brazil.



ORIGINAL ARTICLE

Sampling technique affects the population structure assessments of fiddler crab *Minuca vocator* (Herbst, 1804) (Ocypodidae: Gelasiminae)

Karine Delevati Colpo^{1,2} and Maria Lucia Negreiros-Fransozo³

1 Instituto de Limnología “Dr. Raúl A. Ringuelet”, UNLP-CONICET, Boulevard 120 y 62, Casilla de Correo N° 712, CC: 1900. La Plata, Argentina.

KDC E-mail: kacolpo@ilpla.edu.ar

2 Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.

3 Universidade Estadual Paulista “Júlio de Mesquita Filho”, Instituto de Biociências, Departamento de Zoologia. 18618-970 Botucatu, São Paulo, Brazil.

MLNF E-mail: mlnf@ibb.unesp.br

ZOOBANK <http://zoobank.org/urn:lsid:zoobank.org:pub:81954307-75BB-4747-87DS-976008DC7B39>

ABSTRACT

We examined how the sampling technique can affect the evaluation of *Minuca vocator* (Herbst, 1804) population structure. We used two sampling procedures: catch-per-unit-effort (CPUE) and quadrat technique (QT). Body size, size–frequency distribution, population density, juvenile recruitment rates, proportion of ovigerous females and sex ratio were compared between the sampling procedures. QT allowed us to estimate and compare crab and burrow densities. CPUE sampled both adult crabs and the largest crabs more frequently, whereas QT recorded a greater proportion of smaller crabs. CPUE underestimated the size of *M. vocator* populations, while density estimates obtained with QT were accurate. The proportion of juveniles was higher with QT than with CPUE, suggesting that recruitment rates estimated by QT were more suitable. The sampling effort provided by CPUE was more efficient for obtaining ovigerous-dependent information than QT. Both sampling techniques showed a predominance of males in all three *M. vocator* populations. The population density estimation based on burrows overestimated the natural density of *M. vocator* in all mangroves.

CORRESPONDING AUTHOR

Karine Delevati Colpo
kacolpo@ilpla.edu.ar

SUBMITTED 29 February 2016

ACCEPTED 20 July 2016

PUBLISHED 20 October 2016

Guest Editors

Maria Lúcia Negreiros-Fransozo
and Adilson Fransozo

DOI 10.1590/2358-2936e2016015

Our results suggest that neither CPUE nor QT individually were accurate sampling techniques, but together provided reliable assessments of fiddler crab populations.

KEY WORDS

Body size, catch-per-unit-effort, quadrat, recruitment, sex-ratio.

INTRODUCTION

It is important to assess the abundance of individuals in the field for ecological studies, environmental impact evaluation and conservation biology (Schlacher *et al.*, 2016). Obtaining accurate field information can be difficult, especially in estuarine sediments, where many species are burrowers and sampling time is limited to periods of low tide (Conde and Díaz, 1985; Vermeiren and Sheaves, 2014). Fiddler crabs are usually abundant macrofauna in sediments of tropical and subtropical estuarine environments and play a remarkable role in habitat functioning, as they are ecosystem engineers (Kristensen, 2008). It is therefore essential to obtain precise data on fiddler crab populations in order to learn about their dynamics and effects on the environment.

Excavated quadrats, transect sampling, burrow count, visual observation, hand digging, pitfall trapping, mark-release-recapture estimates, and photography are techniques traditionally used in fiddler crab studies (Johnson, 2003; Vermeiren and Sheaves, 2014), and each has its pros and cons. Excavated quadrat and transect sampling provide accurate density estimates of burrowing crabs (Colby and Fonseca, 1984; Skov and Hartnoll, 2001; Costa and Negreiros-Fransozo, 2003), but take time, and the movement large volumes of sediment may result in a considerable environmental impact on sensitive estuarine habitats (Schlacher *et al.*, 2016). Density estimation by burrow counting tends to overestimate the actual density of crabs, since they can dig more than one burrow (Montague, 1980; Macintosh, 1988; Macia *et al.*, 2001; Skov and Hartnoll, 2001). Quantifying density by visual surface observation may lead to underestimation because some crabs remain inside their burrows (Macintosh, 1988). Hand catch and pitfall trapping require knowledge of crab activity patterns, and are laborious techniques, which could limit replication over a short time (Vermeiren and Sheaves, 2014). Mark-release-recapture techniques are only suitable when captures can be carried out quickly and efficiently

(Hockett and Kritzler, 1972). Photography provides accurate spatial distribution patterns on large spatial scales, but taxonomic differentiation is difficult when sympatric species are morphologically similar (Goshima and Murai, 1998; Vermeiren and Sheaves, 2014). Considering the diversity of sampling protocols, any comparisons should be made with caution (Nobbs and McGuinness, 1999).

Population studies often evaluate density, age/size composition, sex ratio, juvenile recruitment rate, size at onset of sexual maturity, and reproductive period (Colpo and Negreiros-Fransozo, 2004; Lima *et al.*, 2014; Andrade *et al.*, 2015; Hirose *et al.*, 2015). The assessment of some of these population parameters can be affected by the sampling procedure chosen for the study (Macia *et al.*, 2001; Johnson, 2003; Costa and Negreiros-Fransozo, 2003; Hirose *et al.*, 2015). Small crabs can be overlooked by visual observation or hand digging techniques, which would affect the age/size composition and juvenile recruitment estimates (Costa and Negreiros-Fransozo, 2003). Frequency of ovigerous females and hence, the reproductive period, could be underestimated by quadrat, transect or visual observation procedures, since these females usually stay underground and finding them requires a greater capture effort (Macia *et al.*, 2001). Fiddler crab males are more conspicuous than females because of their large cheliped; thus, hand digging and visual observation can promote bias in sex ratio estimation (Johnson, 2003).

Recently, Shih *et al.* (2016) reorganized the subfamily rankings of Ocypodidae and reviewed the taxonomic status of the genus *Uca* Leach, 1814 (*sensu lato*) and its subgenera based on phylogenetic relationships and a large-scale multigene study. Thus, we adopted here such new classification, in which only *Uca maracoani* (Latreille, 1803) in Brazil remained in the former genus and belongs to the Ocypodinae Rafinesque, 1815. Other fiddler crabs, from Brazilian coast, are attributed to *Leptuca* Bott, 1973 or *Minuca*

Bott, 1954 genus, which belong to the Gelasiminae Miers, 1886. Thus, as proposed by Shih *et al.* (2016), the fiddler crabs belonging to Gelasiminae, with occurrence in the Brazilian coast, are the following ones: *Leptuca cumulanta* (Crane, 1943); *Leptuca leptodactyla* (Rathbun, 1898); *Leptuca thayeri* (Rathbun, 1900); *Leptuca uruguayensis* (Nobili, 1901); *Minuca burgersi* (Holthuis, 1967); *Minuca mordax* (Smith, 1870); *Minuca rapax* (Smith, 1870); *Minuca victoriana* (von Hagen, 1987) and *Minuca vocator* (Herbst, 1804).

Considering the importance of obtaining reliable assessments of fiddler crabs, we examined how the sampling technique can affect the evaluation of population structure. To do so, we sampled three *M. vocator* populations in subtropical mangroves using two different sampling procedures: catch-per-unit-effort (CPUE) and quadrat technique (QT). For the three populations, we compared body size, size–frequency distribution, population density, juvenile recruitment rates, proportion of ovigerous females and sex ratio between sampling procedures. QT allowed us to estimate and compare crab and burrow density.

MATERIAL AND METHODS

The fiddler crab *M. vocator* inhabits shaded mud flats in tropical mangroves (Crane, 1975; Colpo and Negreiros-Fransozo, 2004). We sampled this fiddler crab species in three mangroves in São Paulo State, southeastern Brazil: mangrove of the Itapanhau River (23°49'14"S 46°09'14"W), mangrove of the Indaia River (23°24'51"S 45°03'14"W), and mangrove of the Itamambuca River (23°24'43"S 45°01'13"W). The three populations were found in similar habitat conditions. Sampling was carried out monthly from August 1999 to July 2000, during spring low tide.

The sampling procedures used in this study were catch-per-unit-effort (CPUE) and quadrat technique (QT). In each mangrove, an area of 40 m² with dominance of *M. vocator* was selected. Half of this area was sampled using CPUE and the other half using QT. Both procedures were carried out on the same sampling day. In the CPUE procedure, an experienced collector moved randomly over the sampling area for 15 minutes, extracting crabs from their burrows using a diving knife. In the QT procedure, a 0.80 m² wooden frame was used [quadrat size follows Green (1979)]. Three random replications of the quadrat were

performed in the sampling area every month. First, the number of burrows was recorded, after which the crabs were sampled by excavation. The collector spent about 15 minutes capturing fiddler crabs in QT; thus, both sampling procedures took similar times.

Samples obtained by each sampling procedure were treated separately in the laboratory. All fiddler crabs were identified, measured (carapace width – CW), and their sex was determined. We also checked females for eggs.

In order to evaluate differences in the population structure assessments, we compared body size, size–frequency distribution, population density, juvenile's recruitment rate, proportion of ovigerous females and sex ratio of *M. vocator* collected with both sampling procedures. For each population, crab size (CW) was compared between sampling procedures by a Mann-Whitney test (Sokal and Rohlf, 1979). Size frequency distributions of crabs collected using CPUE and QT were compared within populations by Kolmogorov-Smirnov test (Sokal and Rohlf, 1979). Monthly estimates were made of the approximate density of *M. vocator* (m²) obtained by each procedure (CPUE and QT) based on the number of crabs collected in the sampling area destined to each (20 m²). The densities provided by each sampling procedure were compared within each of the three populations by Mann-Whitney test (Sokal and Rohlf, 1979).

The proportion of juveniles was calculated monthly from the total number of crabs sampled with each technique. These proportions were compared each month by calculating the z statistic for a paired comparison using the normal approximation of the binomial distribution (Sokal and Rohlf, 1979). We considered as juveniles any crabs with CW smaller than the smallest ovigerous female in each population (Colpo and Negreiros-Fransozo, 2003). The proportion of ovigerous crabs was calculated monthly from the total adult females captured with each sampling procedure. The frequency of ovigerous females with relation to time suggests the breeding season, so we evaluated the number of months during which they were found using CPUE and QT. A chi-square test was used to evaluate deviations in sex ratio (1male:1female) in each population, and the male ratio obtained using each sampling technique was compared by a z test, as described for the proportion of juveniles.

Using the data obtained with QT, we compared the density of burrows with the density of *M. vocator* monthly using Student's test (Sokal and Rohlf, 1979). A statistical significance level of 5% was used in all analyses.

RESULTS

The fiddler crabs sampled by CPUE were larger than those sampled by QT in all populations (Mann-Whitney test, $p < 0.001$) (Fig. 1). However, both sampling procedures showed the same size trend among populations, since *M. vocator* reaches larger sizes in Itamambuca than in Indaia and Itapanhau. The size–frequency distributions observed with CPUE differed from the size distribution pattern recorded with QT for all study populations (Kolmogorov-Smirnov test, $p < 0.01$) (Fig. 2). A greater number of smaller crabs was sampled with QT, while the larger crabs were obtained with CPUE (Fig. 2). Although CPUE provided more crabs than QT (Fig. 2), the density measures obtained by QT were higher than those obtained by CPUE in Indaia and Itamambuca

(Fig. 3). In Itapanhau, we observed the same trend, although there was no statistic difference between procedures. Fig. 3 shows that data obtained by QT had greater dispersion than data obtained by CPUE.

The comparison of juvenile recruitment also showed that smaller crabs were more efficiently sampled by QT than CPUE in most months, in all three mangroves (z test, $p < 0.05$) (Fig. 4). Nevertheless, both sampling procedures showed similar year-round recruitment pattern for all three populations, since CPUE and QT suggested continuous recruitment for all study populations (Fig. 4). CPUE was more effective than QT for recording ovigerous females (Fig. 5). CPUE found that the percentage of adult females that were ovigerous was 22.4% in Itapanhau, 9.3% in Indaia, and 10.3% in Itamambuca, while QT only found ovigerous females in Itamambuca (8.9% of adult females). Furthermore, CPUE suggested a continuous breeding season at Itapanhau and Itamambuca, since we recorded ovigerous females in nine months of the sampling year. Both sampling procedures indicated prevalence of males, except for the sample obtained by QT in Itamambuca, in which the sex ratio did not

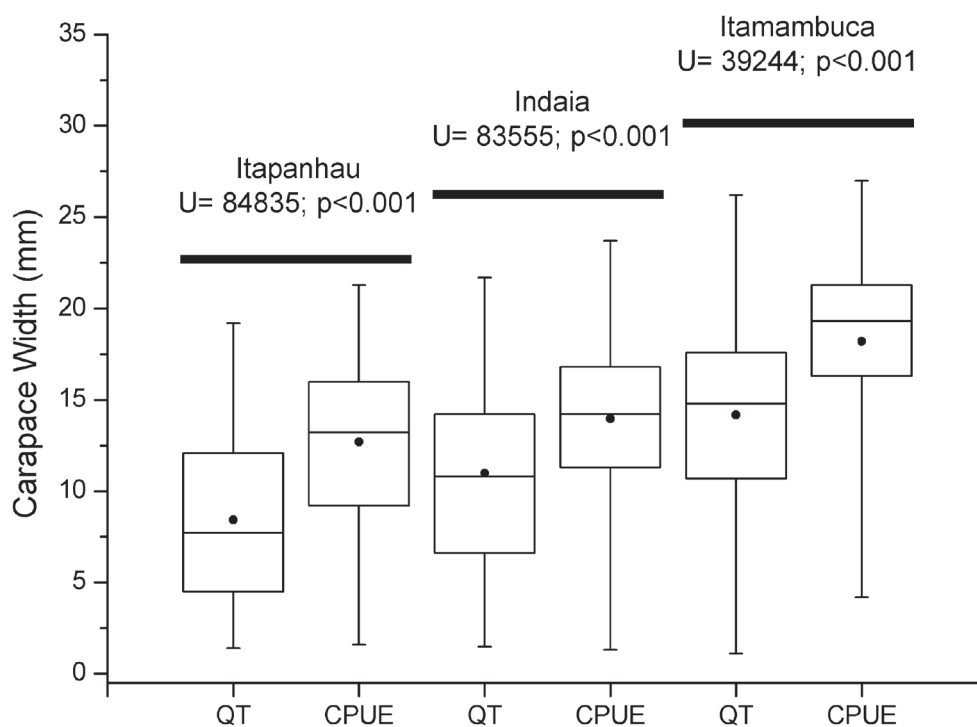


Figure 1. *Minuca vocator* (Herbst, 1804). Body size comparisons (CW mm) between sampling procedures, within each population (U – Mann-Whitney test). CPUE, catch-per-unit-effort. QT, quadrat technique. Mean, Median, 25–75%, Min–Max.

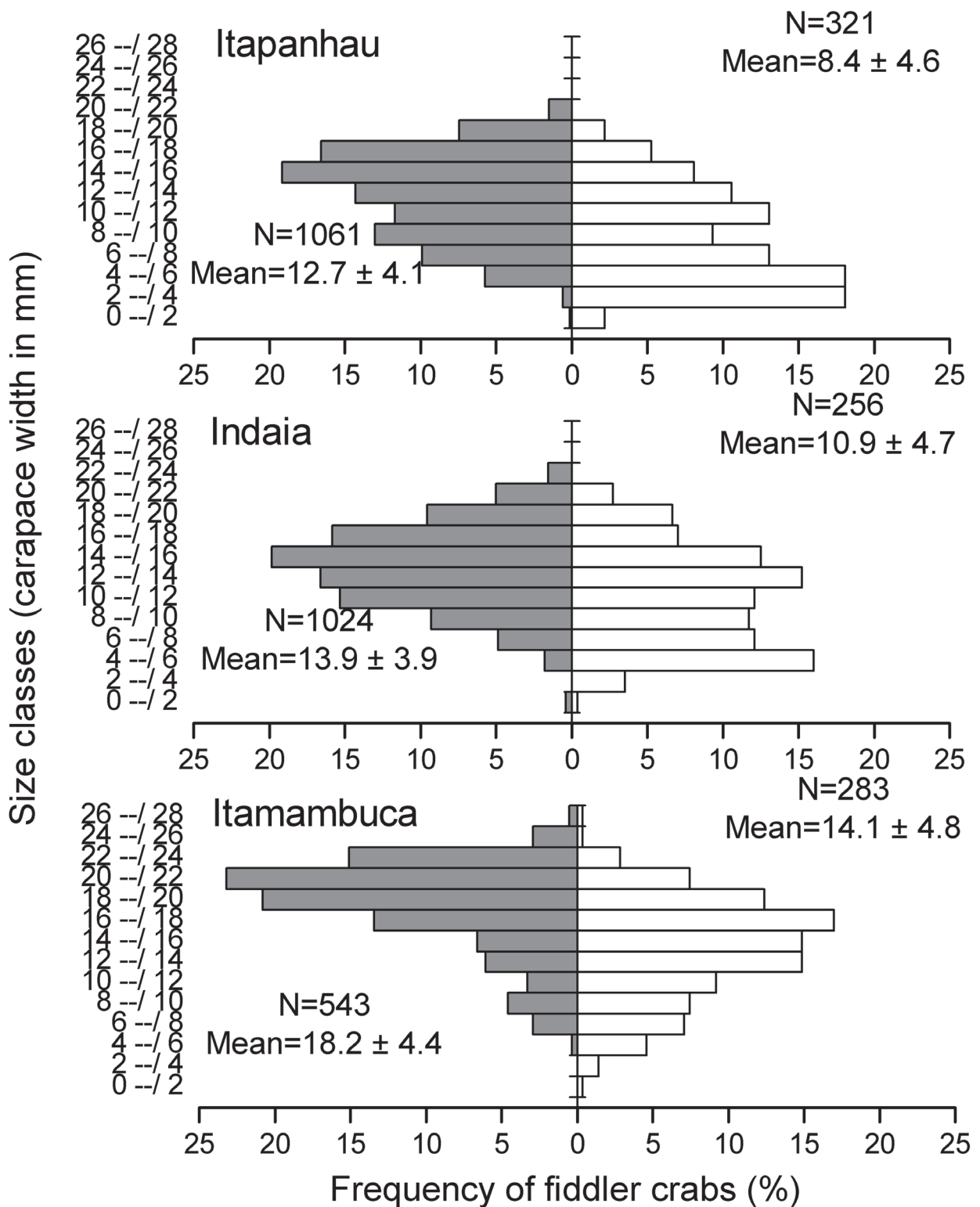


Figure 2. *Minuca vocator* (Herbst, 1804). Size–frequency distribution obtained by CPUE (catch–per–unit–effort – gray bars) and QT (quadrat technique – white bars) in each population. N= total number of sampled fiddler crabs. Mean and standard deviation of population (carapace width – mm).

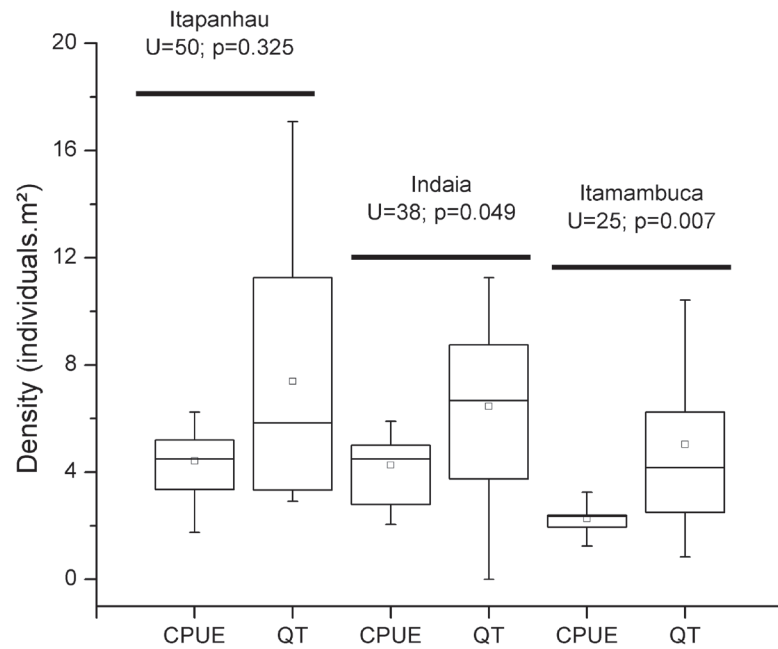


Figure 3. *Minuca vocator* (Herbst, 1804). Density comparisons (fiddler crab .m²) between sampling procedures, within each population (U – Mann-Whitney test). CPUE, catch-per-unit-effort. QT, quadrat technique. Mean, Median, 25–75%, Min–Max.

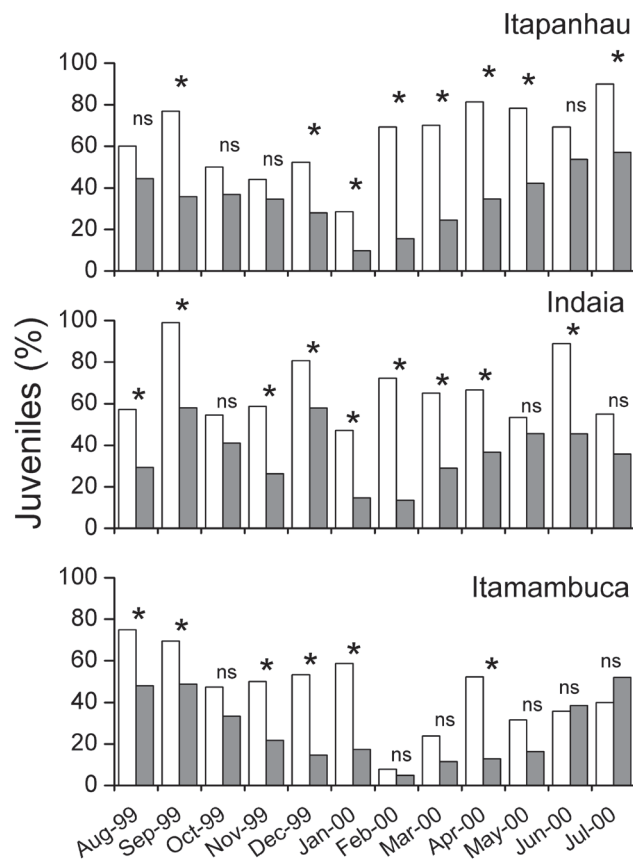


Figure 4. *Minuca vocator* (Herbst, 1804). Comparisons between proportions of juveniles obtained by CPUE (catch-per-unit-effort – gray columns) and QT (quadrat technique – white columns) throughout the year, in the studied mangroves. *, statistical significance. ns, no significant (z test).

show any difference (Tab. 1). Male rates did not differ between the sampling procedures in all populations (z test; $p > 0.05$).

The QT procedure allowed us to compare the density of burrows with the density of *M. vocator*. We recorded

a mean 45.1 burrows.m⁻² at Itapanhau (burrows: individuals ratio, 4.8:1), 24 burrows.m⁻² at Indaia (3.7:1), and 34.9 burrows.m⁻² at Itamambuca (7:1). Burrow density was higher than *M. vocator* density in most months (Student's t test $p < 0.05$) (Fig. 6).

Table 1. *Minuca vocator* (Herbst, 1804). Sex ratio (males: females) in each mangrove and sampling procedure. CPUE: catch-per-unit-effort. QT: quadrat technique. *, Chi-Square test significance ($p < 0.05$).

Mangroves	Sampling procedures	
	CPUE	Quadrat
Itapanhau	1.25 : 1*	1.91 : 1*
Indaia	1.67 : 1*	1.29 : 1*
Itamambuca	1.28 : 1*	0.9 : 1

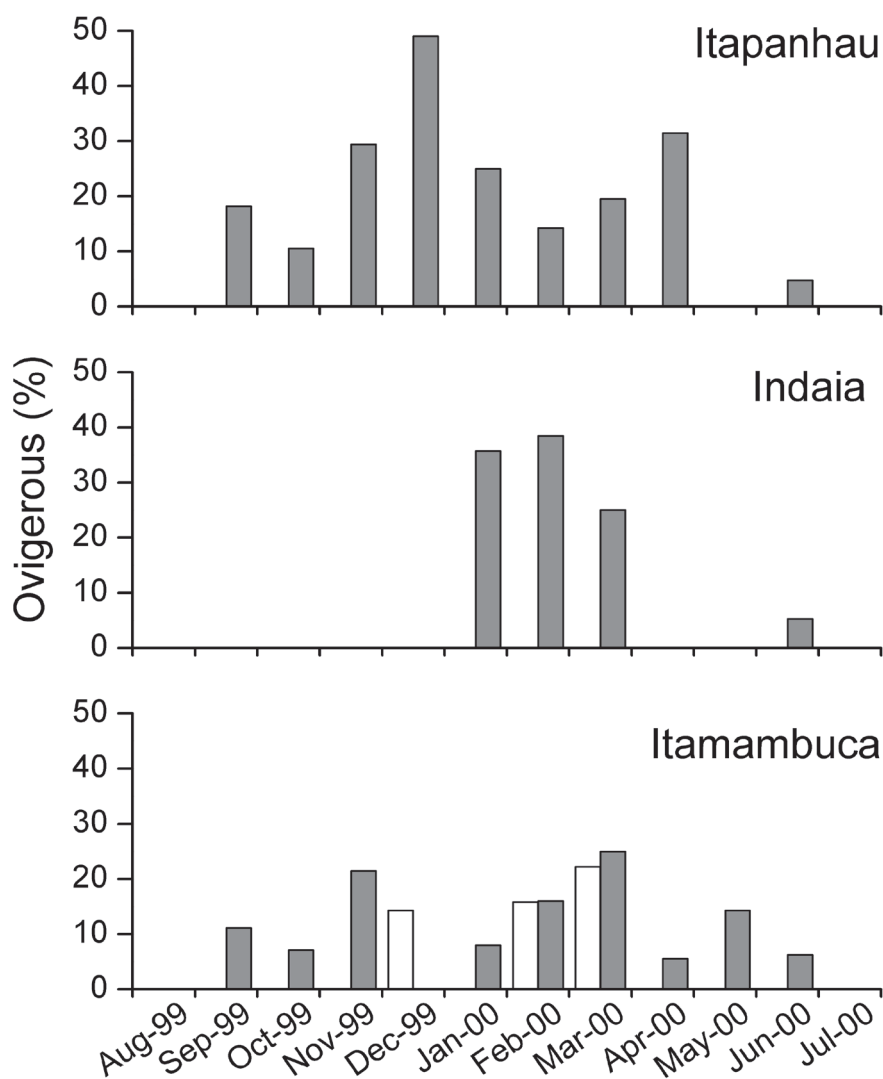


Figure 5. *Minuca vocator* (Herbst, 1804). Proportion of ovigerous females sampled by CPUE (catch-per-unit-effort – gray columns) and QT (quadrat technique – white columns) throughout the year, in the studied mangroves.

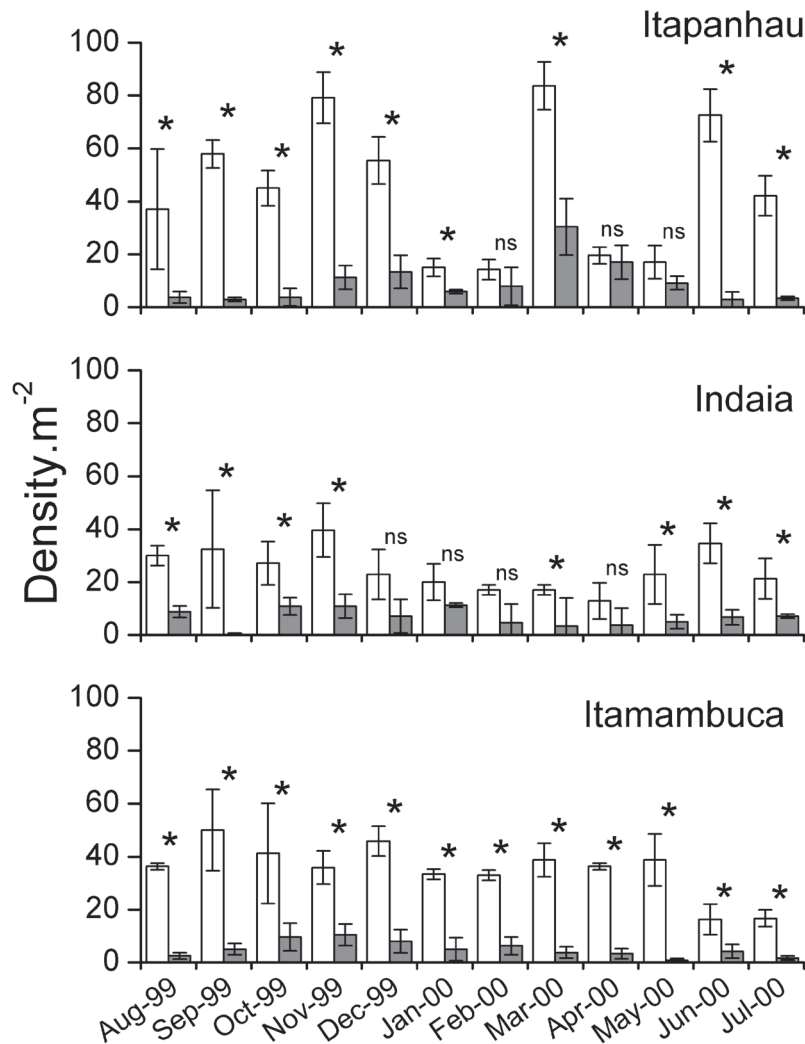


Figure 6. Mean density (standard deviation) of burrows (white columns) and *Minuca vocator* (Herbst, 1804) (gray columns), recorded with quadrat technique (QT) throughout the year, in the studied mangroves. *, statistical significance. ns, no significant (Student's test).

DISCUSSION

Our results suggest that sampling procedure can induce differences in estimates of population structure in fiddler crabs. Body size estimation and frequency distribution obtained by each sampling procedure did not coincide within populations. Using CPUE, adult crabs and the largest crabs were sampled more frequently, while using QT, a greater proportion of smaller crabs was found, showing that these population parameters were influenced by the sampling technique. Costa and Negreiros-Fransozo (2003), studying *L. thayeri*, also sampled larger fiddler crabs using the CPUE procedure. This suggests that a better estimate

of crab sizes may be achieved by combining the data obtained using both sampling procedures.

Since in QT, the quadrat area was exhaustively scanned for *M. vocator* specimens, we assumed that the density estimates thereby obtained were accurate (Skov and Hartnoll, 2001). Although CPUE is often used as an abundance index (Richards and Schnute, 1986), we considered that it underestimated the size of *M. vocator* populations, despite the higher total number of fiddler crabs sampled with this procedure (Fig. 2). Richards and Schnute (1986) also showed that CPUE was a poor abundance estimator for marine species. Additionally, based on the spread of data recorded with each procedure, we could assume different spatial

distribution patterns for *M. vocator*. CPUE suggests a uniform or random distribution, while QT infers some degree of aggregation (Taylor, 1961; Kristensen *et al.*, 2013). More specific studies are required to define the actual distribution pattern of *M. vocator*.

Settlement and subsequent recruitment to the adult population are processes that influence the population dynamics and densities of intertidal crabs (Flores *et al.*, 2002; Émond *et al.*, 2015). Precise information on juvenile density is therefore central to population ecology, but accurate estimations are difficult to obtain due to sampling constraints (Skov and Hartnoll, 2001; Almeida *et al.*, 2008). Flores *et al.* (2002) used a corer-type sampler (15 cm diameter and 10 cm deep), a sieve to sort sediment (upper 3-cm layer of a quadrat), and visual scanning of the surface for *Perisesarma guttatum* (A. Milne-Edwards, 1869) juveniles in a mangrove area. They found that the latter procedure provided the best results with less sampling effort. Almeida *et al.* (2008) assessed that the recruitment rates for *Carcinus maenas* (Linnaeus, 1758) estimated by pitfall traps were not related to natural densities of the species. In our study, both sampling procedures recorded the same continuous recruitment pattern for all three populations of *M. vocator*. However, the proportion of juveniles obtained with QT was higher than with CPUE, suggesting that recruitment rates estimated by QT were more suitable.

The presence of juveniles all year round indicates a continuous breeding season for *M. vocator*. In tropical and subtropical mangroves, fiddler crabs usually exhibit continuous reproduction, probably due to the constancy of environmental conditions and resource availability throughout the year (Colpo and Negreiros-Fransozo, 2004; Litulo, 2005; Benetti *et al.*, 2007; Costa and Soares-Gomes, 2009; Martins and Masunari, 2013). The data on ovigerous frequency obtained by CPUE corroborated the continuous breeding hypothesis in Itapanhau and Itamambuca. However, the proportion of ovigerous females found by QT was very low and did not enable a suitable estimation of the reproductive period. As a broad-front species, *M. vocator* remains in the burrow while eggs are incubating (Crane, 1975; How *et al.*, 2009; Ribeiro *et al.*, 2010), which hinders ovigerous female sampling. CPUE appears to have been more efficient for providing ovigerous-dependent information than QT. At Indaia, the high recruitment rate contrasted with the low proportion of ovigerous

females. This population may depend on larvae supply from a neighboring population (Bogazzi *et al.*, 2001; Laurenzano *et al.*, 2012).

In general, both sampling techniques showed predominance of males in all three *M. vocator* populations. The sex ratio biased in favor of males is a widely accepted trend for adult fiddler crabs, since male dominance has been recorded for many species collected by different sampling procedures (Johnson, 2003). The causes of this sex ratio pattern are historically related to differential growth rates, migration, spatial and temporal variation in the use of resources, and differential behavior patterns related to sex (Montague, 1980; Salmon, 1987; Caravello and Cameron, 1987; Spivak *et al.*, 1991; Macia *et al.*, 2001; Costa and Negreiros-Fransozo, 2003; Hayes *et al.*, 2013). However, Johnson (2003) concluded that high female mortality rate, probably due their high energy investment in reproduction, is the principal cause of the notable sex ratio bias toward males in fiddler crabs populations.

Mangrove ocypodids start burrowing in the post-settlement stage (Macintosh, 1988; Kristensen, 2008). It would be possible to evaluate seasonal changes in size composition of the population through the density and size of burrows; however, estimates may be somewhat skewed. Skov and Hartnoll (2001) found a highly significant coefficient of determination ($r^2 = 0.98$) for carapace width and burrow diameter in *Uca annulipes* (H. Milne Edwards, 1837) [= *Austruca perplexa* (H. Milne Edwards, 1852) as mentioned by Shih *et al.*, 2016]. However, Macia *et al.* (2001) observed that burrow counting, for this same fiddler crab species, overestimated the population by 25%. Recently, Schlacher *et al.* (2016) reviewed the accuracy of density estimation by means of burrow entrance counts. They found no relationship between number of burrows and population size. There is thus considerable uncertainty in predicting the density of benthic organisms according to the number of holes. In this study, the population density estimation based on burrows overestimated the natural density of *M. vocator* in all mangroves. The higher number of burrows than the existing number of fiddler crabs may be because they dig more than one burrow to escape from predators, to avoid conspecific aggression, or even that they abandoned or lost their burrows (Macintosh, 1988). Additionally, *M. vocator*

burrows have two entrances (personal observation), leading to overestimations of burrow density. Another point to consider is that other fiddler crab species were found coexisting with *M. vocator* in the sampling areas (*L. thayeri*, *L. uruguayensis*, *M. mordax*, *M. rapax*, and *M. burgersi*). Of the total fiddler crabs collected by QT, *M. vocator* represented 83% at Itapanhau, 73% at Indaia and 51% at Itamambuca. Evidently, some of the counted holes were not burrowed by *M. vocator*. The presence of sympatric burrowing species also discredits the use of indirect census techniques to measure population sizes.

To sum up, the accurate estimation of body size and size–frequency distribution requires the combination of data obtained by both CPUE and QT procedures. QT provided a reliable evaluation of population density and juvenile recruitment rates, whereas CPUE was more efficient for providing ovigerous-dependent information. However, the sex ratio in the study populations favored males, regardless of the sampling procedure. These results suggest that neither CPUE nor QT individually were accurate sampling techniques, but together provided reliable assessments of fiddler crab populations. The choice of an appropriate sampling procedure thus depends on the study goals, work scale, sampling time, existence of sympatric species and kind of environment.

ACKNOWLEDGEMENTS

This paper is dedicated to Professor Nilton J. Helbling who has inspired generations of Brazilian carcinologists. We thank CNPq for a fellowship to the first author, FAPESP (#98/03134-6) for financial support to the second author, SESC (Bertioga) for providing lodging, and NEBECC co-workers for their assistance with field work. All samplings were in accordance with Brazilian State and Federal laws concerning wild animals.

REFERENCES

- Almeida, M.J.; Flores, A.A.V. and Queiroga, H. 2008. Effect of crab size and habitat type on the locomotory activity of juvenile shore crabs, *Carcinus maenas*. *Estuarine, Coastal and Shelf Science*, 80(4): 509–516.
- Andrade, L.S.; Frameschi, I.F.; Castilho, A.L.; Costa, R.C. and Fransozo, A. 2015. Can the pattern of juvenile recruitment and population structure of the speckled swimming crab *Arenaeus cribrarius* (Decapoda: Brachyura) be determined by geographical variations? *Marine Ecology*, 36(4): 950–958.
- Benetti, A.S.; Negreiros-Fransozo, M.L. and Costa, T.M. 2007. Population and reproductive biology of the crab *Uca burgersi* (Crustacea: Ocypodidae) in three subtropical mangrove forests. *Revista de Biología Tropical*, 55(1): 55–70.
- Bogazzi, E.; Iribarne, O.; Guerrero, R. and Spivak, E. 2001. Wind pattern may explain the Southern limit of distribution of a Southwestern Atlantic fiddler crab. *Journal of Shellfish Research*, 30(1): 356–360.
- Caravello, H.E. and Cameron, G.N. 1987. Foraging time allocation in relation to sex by the gulf coast fiddler crab (*Uca panacea*). *Oecologia*, 72(1): 123–126.
- Colby, D. and Fonseca, M. 1984. Population dynamics, spatial dispersion and somatic growth of the sand fiddler crab *Uca pugilator*. *Marine Ecology Progress Series*, 16: 262–279.
- Colpo, K.D. and Negreiros-Fransozo, M.L. 2003. Reproductive output of *Uca vocator* (Herbst, 1804) (Brachyura, Ocypodidae) from three subtropical mangroves in Brazil. *Crustaceana*, 76(1): 1–11.
- Colpo, K.D. and Negreiros-Fransozo, M.L. 2004. Comparison of the population structure of the fiddler crab *Uca vocator* (Herbst, 1804) from three subtropical mangrove forests. *Scientia Marina*, 68(1): 139–146.
- Conde, J.E. and Díaz, H. 1985. Diseño de muestreo aleatorio estratificado aplicado al estudio de poblaciones del género *Uca* (Brachyura, Ocypodidae). *Investigaciones Pesqueras*, 49(4): 567–579.
- Costa, T.M. and Negreiros-Fransozo, M.L. 2003. Population biology of *Uca thayeri* Rathbun, 1900 (Brachyura, Ocypodidae) in a subtropical South American mangrove area: results from transect and catch-per-unit-effort techniques. *Crustaceana*, 75(10): 1201–1218.
- Costa, T.M. and Soares-Gomes, A. 2009. Population structure and reproductive biology of *Uca rapax* (Decapoda: Ocypodidae) in a tropical coastal lagoon, southeast Brazil. *Zoologia*, 26(4): 647–657.
- Crane, J. 1975. Fiddler crabs of the world, Ocypodidae: genus *Uca*. Princeton, Princeton University Press, 736p.
- Émond, K.; Sainte-Marie, B.; Galbraith, P.S. and Bêty, J. 2015. Top-down vs. bottom-up drivers of recruitment in a key marine invertebrate: investigating early life stages of snow crab. *Journal of Marine Science*, 72(5): 1336–1348.
- Flores, A.A.V.; Saraiva, J. and Paula, J. 2002. Sexual maturity, reproductive cycles and juvenile recruitment of *Perisesarma guttatum* (Brachyura, Sesamidae) at Ponta Rasa mangrove swamp, Inhaca Island, Mozambique. *Journal of Crustacean Biology*, 22(1): 143–156.
- Goshima, S. and Murai, M. 1998. Mating investment of male fiddler crabs, *Uca lactea*. *Animal Behaviour*, 36(4): 1249–51.
- Green, R.H. 1979. Sampling design and statistical techniques for environmental biologists. New York, Wiley and Sons, 257p.
- Hayes, C.L.; Booksmythe, I.; Jennions, M.D. and Backwell, P.R.Y. 2013. Does male reproductive effort increase with age? Courtship in fiddler crabs. *Biology Letters*, 9(2): 20121078.

- Hirose, G.L.; Souza, L.S.; Silva, S.L.R.; Alves, D.F.R. and Negreiros-Fransozo, M.L. 2015. Population structure of the red mangrove crab, *Goniopsis cruentata* (Decapoda: Grapsidae) under different fishery impacts: Implications for resource management. *Revista de Biología Tropical*, 63(2): 443–457.
- Hockett, J.C. and Kritzler, H. 1972. Capture-recapture techniques with *Uca*. *Biological Bulletin*, 142(1): 49–56.
- How, M.J.; Zeil, J. and Hemmi J.M. 2009. Variability of a dynamic visual signal: the fiddler crab claw-waving display. *Journal of Comparative Physiology A*, 195(1): 55–67.
- Johnson, P. 2003. Biased sex ratios in fiddler crabs (Brachyura, Ocypodidae): A review and evaluation of the influence of sampling method, size class, and sex-specific mortality. *Crustaceana*, 76(5): 559–580.
- Kristensen, E. 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *Journal of Sea Research*, 59(1–2): 30–43.
- Kristensen, E.; Delefosse, M.; Quintana, C.O.; Banta, G.T.; Petersen, H.C. and Jørgensen, B. 2013. Distribution pattern of benthic invertebrates in Danish estuaries: The use of Taylor's power law as a species-specific indicator of dispersion and behavior. *Journal of Sea Research*, 77: 70–78.
- Laurenzano, C.; Fariás, N.E. and Schubart, C.D. 2012. Mitochondrial genetic structure of two populations of *Uca uruguayensis* fails to reveal an impact of the Rio de la Plata on gene flow. *Nauplius*, 20(1): 15–25.
- Lima, P.A.; Fransozo, V.; Andrade, L.S.; Almeida, A.C.; Furlan, M. and Fransozo, A. 2014. Distribution and population structure of the flecked box crab *Hepatus pudibundus* (Decapoda, Brachyura) in the western South Atlantic. *Marine Biology Research*, 10(6): 589–600.
- Litulo, C. 2005. Population biology of the fiddler crab *Uca annulipes* (Brachyura: Ocypodidae) in a tropical East African mangrove (Mozambique). *Estuarine, Coastal and Shelf Science*, 62(1): 283–290.
- Macia A.; Quincardete, I. and Paula, J. 2001. A comparison of alternative techniques for estimating population density of the fiddler crab *Uca annulipes* at Saco mangrove, Inhaca Island (Mozambique), p. 213–219. In: J. Paula; A.A.V. Flores and C. Fransen (eds), *Advances in Crustacean Research. Proceedings of the 7th Colloquium Crustacea Decapoda Mediterranea. Hydrobiology / Advances in Hydrobiology*, vol. 449. The Netherlands, Kluwer Publishers.
- Macintosh, D.J. 1988. The ecology and physiology of decapods of mangrove swamps. *Symposium of the Zoology Society of London*, 59: 315–341.
- Martins, S.B. and Masunari, S. 2013. Temporal distribution in the abundance of the fiddler crab *Uca (Leptuca) uruguayensis* Nobili, 1901 (Decapoda: Ocypodidae) from Garças River mangrove, Guaratuba Bay, southern Brazil. *Nauplius*, 21(2): 151–159.
- Montague, C.L. 1980. A natural history of temperate western Atlantic fiddler crabs (genus *Uca*) with reference at their impact on the salt marsh. *Contributions in Marine Science*, 23: 25–55.
- Nobbs, M. and McGuinness, K.A. 1999. Developing techniques for quantifying the apparent abundance of fiddler crabs (Ocypodidae: *Uca*) in mangrove habitats. *Australian Journal of Ecology*, 24(1): 43–49.
- Ribeiro, P.D.; Daleo, P. and Iribarne, O. 2010. Density affects mating mode and large male mating advantage in a fiddler crab. *Oecologia*, 164(4): 931–941.
- Richards, L.J. and Schnute, J.T. 1986. An experimental and statistical approach to the question: is CPUE an index of abundance? *Canadian Journal of Fisheries and Aquatic Sciences*, 43(6): 1214–1227.
- Salmon, M. 1987. On the reproductive behavior of the fiddler crab *Uca thayeri*, with comparisons to *U. pugilator* and *U. vocans*: evidence for behavioral convergence. *Journal of Crustacean Biology*, 7(1): 25–44.
- Schlacher, T.A.; Lucrezi, S.; Peterson, C.H.; Connolly, R.M.; Olds, A.D.; Althaus, F.; Hyndes, G.A.; Maslo, B.; Gilby, B.L.; Leon, J.X.; Weston, M.A.; Lastra, M.; Williams, A. and Schoeman, D.S. 2016. Estimating animal populations and body sizes from burrows: Marine ecologists have their heads buried in the sand. *Journal of Sea Research*, 112: 55–64.
- Shih, H.; Ng, P.K.L.; Davie, P.J.F.; Schubart, C.D.; Türkay, M.; Naderloo, R.; Jones, D. and Liu, M-Y. 2016. Systematics of the family Ocypodidae Rafinesque, 1915 (Crustacea: Brachyura), based on phylogenetics relationships, with a reorganization of subfamily rankings and a review of the taxonomic status of *Uca* Leach, 1814, *sensu lato* and its subgenera. *Raffles Bulletin of Zoology*, 64: 139–175.
- Skov, M.W. and Hartnoll, R.G. 2001. Comparative suitability of binocular observation, burrow counting and excavation for the quantification of the mangrove fiddler crab *Uca annulipes* (H. Milne Edwards). p. 201–212. In: J. Paula; A.A.V. Flores and C. Fransen (eds), *Advances in Crustacean Research. Proceedings of the 7th Colloquium Crustacea Decapoda Mediterranea. Hydrobiology / Advances in Hydrobiology*, vol. 449. The Netherlands, Kluwer Publishers.
- Sokal, R.R. and Rohlf, F.J. 1979. *Biometry*, 3rd ed. New York, W.H. Freeman and Co., 880p.
- Spivak, E.D.; Gavio, M.A. and Navarro, C.E. 1991. Life history and structure of the world's southernmost *Uca* population: *Uca uruguayensis* (Crustacea, Brachyura) in Mar Chiquita lagoon (Argentina). *Bulletin of Marine Science*, 48(3): 679–688.
- Taylor, L.R. 1961. Aggregation, variance and the mean. *Nature*, 189: 732–735.
- Vermeiren, P. and Sheaves, M. 2014. A remote photographic technique for high replication, large scale understanding of spatial distribution patterns of intertidal crabs. *Hydrobiologia*, 724(1): 79–89.