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Ecomorphological Adaptations of Second Maxilliped-setation: Insights from Three Species of Fiddler Crabs from Panama

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The functional morphology of maxilliped-setation in three species of fiddler crabs—*Petruca panamensis*, *Leptuca terpsichores* and *L. beebei*—collected from Panama were studied using a comparative ecomorphological approach. The coverage of spoon-tipped (ST) and plumose (P) setae on the inner surface of the second maxilliped were noted, and the abundance of each setal type was enumerated, with crab carapace width as the covariate. These attributes were then related to the sediment particle size characterization of their respective collection sites for an ecomorphological comparison. All three species have mixed setation, albeit in different proportions of coverage. For *L. terpsichores*, the ST:P coverage was consistently ca. 70%:30% whereas there was approximately equal coverage of both setal types (*i.e.*, 50% ST:50% P) on the maxillipeds of *L. beebei* and *P. panamensis*. Analysis of Covariance (ANCOVA) results of setal counts between the sexes in each species showed that the number of ST and P setae did not differ significantly between males and females, indicating an absence of sexual dimorphism in mouthpart setae. When all three species were compared—sexes combined within each species—ANCOVA results reveal that for any crab of a given size, there were significantly more ST setae on the second maxilliped of *L. terpsichores* (sediment from sampling site classified as 'moderately-sorted medium sand') than *L. beebei* (sediment from sampling site classified as 'moderately-sorted fine sand') and *P. panamensis* (a rocky-habitat species); no significant difference was detected between ST abundance in the latter two species. Current results provide unequivocal quantitative evidence that the abundance of ST setae can be an indicator to differentiate habitats down to the level of different sand-grain size, *i.e.*, medium sand versus fine sand habitats of *L. terpsichores* and *L. beebei*, respectively. Both *L. beebei* and *P. panamensis* had significantly fewer ST setae than *L. terpsichores*, possibly because the former two species' habitats have sediments with sand grains that are less coarse than the latter's. On rocks, *P. panamensis* does not produce pseudofecal pellets as they directly swallow food materials pinched from the rock surfaces without sorting, rendering the role of ST setae of secondary importance. The three species did not differ significantly in P setae abundance, suggesting that the adaptive function of this type of setae to habitat characteristics remains debatable. The significance of ST setae as an ecomorphological adaptation for efficient food extraction from sandy sediments is, thus, evident in *L. terpsichores*. As for other two species—*L. beebei* and *P. panamensis*—that live in environments with finer sediment grain sizes, the adaptive role of ST setae is of diminished functional importance. Fiddler crab species with mixed setal types may have greater potential to exhibit feeding plasticity should their habitats be threatened.

Key words: Crustacean mouthparts, Functional morphology, Habitat adaptation, Plumose setae, Spoon-tipped setae.

BACKGROUND

Comparative biology is the study of interspecific similarities and differences in traits. It uses natural variations and disparities to understand the patterns of life, from genes to communities, as well as the critical role of organisms in ecosystems. This field encompasses many disciplines in the biological sciences, such as behavioral ecology, ecophysiology and ecomorphology. While behavioral ecology is driven by optimality models (*e.g.*, Krebs and Davies 1978) and ecophysiology is studied mainly via laboratory experimentation (*e.g.*, Feder et al. 1987), ecomorphology tends to be more correlative and observational (see Wainwright and Reilly 1994). However, ecomorphological studies can contribute insights into the role of biotic and abiotic factors in determining the distributional limits of different species (see Norton et al. 1995).

There are many factors that govern the distribution and abundance of organisms, one of the most important limiting factors being the availability of food resources for basic survival. Crane (1975) in her monumental monograph on the fiddler crabs of the world, reported that these crustaceans are diversified in their exploitation of various biotopes (*e.g.*, sandy, muddy, and rocky substrata, open and vegetated flats, intertidal and supralittoral zones, and from seawater, brackish water to almost freshwater habitats). The adaptive radiation of this brachyuran group was attributed to the modifications of their morphology, behavior, and physiology, to suit the biotopes in which they live (Crane 1975; Murai et al. 1982; Christy and Salmon 1984; Takeda et al. 1996 2004; Zeil and Hemmi 2006).

Fiddler crabs are deposit-feeding macrofauna that extract particulate organic matter, microalgae, bacteria, and other small organisms from the sediment that they process through their mouthparts (Miller 1961; Icely and Jones 1978). Although setae are found on most parts of the crustacean anatomy, the greatest diversity in form and function can be seen on the mouthparts (Sahlmann et al. 2011). Setae present on the maxillipeds of fiddler crabs play an important role in the sorting of food particles (Miller 1961). Spoon-tipped (ST) setae have randomly arranged setules on the proximal end and two rows of serrated denticles on the distal end, giving them their cupped shape, whereas, plumose (P) setae, have two rows of setules located on opposite sides of the setae, giving them their feather-like appearance (Garm 2004). Simultaneous occurrences of both types of setae in fiddler crab species are common, but the relative abundance of each type of setae differ according to the habitat in which they live (Checon and Costa 2017). Crane (1975) described anecdotally that species living in sandy habitats generally have more ST setae while those living in muddy habitats have more P setae present on the second maxillipeds. Based on the ability to extract organic material, ST setae are reported to improve extraction of food from coarser sediments in sandy habitats, while P setae are more effective in obtaining food from muddy sediments (Miller 1961). Although Garm (2004) suggested that P setae do not contact food particles but instead assist in current generation which suspends sediments for extraction of food material, his observations were based on the examination of the mouthpart setae of seven species of decapod crustaceans (prawn, shrimps, crayfish, lobster, hermit crab, green crab), not inclusive of fiddler crabs. Hence, there is a need for comparative studies of P setation to better understand the food procurement process of fiddler crabs in diverse habitats.

Numerous studies on the adaptation of maxilliped-setation in relation to habitat have been conducted in several species of fiddler crabs from various parts of the world (*e.g.*, Icely and Jones 1978; Yamaguchi and Ogata 2000; Lim 2004; Lim and Kalpana 2011; Colpo and Negreiros-Fransozo 2013). These studies provide quantitative evidence supporting Crane's generalization that modification of setation on the second maxilliped is correlated with habitat sediment characteristics. In Panama, two species of fiddler crabs, *Leptuca terpsichores* and *L. beebei*, can be found along the intertidal coastal shore near the old Rodman Naval Base in distinct microhabitats, while another species, *Petruca panamensis*. lives among the stones at the end of the beach at Punta Culebra. The typical biotopes occupied by these three species have been described by Crane (1975) as sandy beaches, sandy-muddy shores, and rocky headlands at the ends of beaches where the sand gives way to a stony habitat, respectively. Currently, there is no literature on the maxilliped setation in these two *Leptuca* species of fiddler crabs while only qualitative information on the maxilliped setation on *P. panamensis* was reported by Takeda and Murai (2003). Hence, the three species present an opportunity to further investigate the ecomorphological adaptations of their mouthpart setation since they live in distinctly different habitats.

One of the distinctive features of fiddler crabs is the sexually dimorphic major cheliped of male fiddler crabs. which is deemed to be useless for feeding (Crane 1975). This means that females can forage for food with two chelipeds while males only use one, leading Weissburg (1991) to hypothesize that females might have more adaptive setae on their first and second maxillipeds to process larger quantities of sediments brought in by two chelipeds. In recent years, there have been substantial evidence from work on *Uca annulipes* and *U. vocans* (see Lim 2004) as well as *U. perplexa*

and *U. vomeris* (see Lim and Kalpana 2011), that there is no sexual dimorphism with regards to maxilliped setation abundance. In this study, we quantify the two types of setae on the second maxilliped—ST setae and P setae—in three species of fiddler crabs from different habitats, to determine if there is sexual dimorphism within each species as well as interspecific similarities and/or differences that relate to ecomorphological adaptations.

MATERIALS AND METHODS

The three species of fiddler crabs used in this study were caught from the coastal shore near the old Rodman Naval Base, and from the rocky shore at Punta Culebra, Panama, in August 2010. *Leptuca terpsichores* and *L. beebei* are commonly found in sandy, and sandy-muddy habitats, respectively while *Petruca panamensis* inhabits rocky shores. Sediment samples (triplicates) from each of the habitats in which the two *Leptuca* species lived were collected and frozen. No sediment was collected from the rocks and stones where *P. panamensis* lives as it was too invasive to scrape the surfaces where the crabs fed. It is noted that each of the three species has a very narrow range of sediment types on which they are found (J Christy personal communication).

Crab specimens were collected, preserved in 75% ethanol, and brought back to the Ecology Laboratory at the National Institution of Education, Nanyang Technological University, Singapore, for further studies. For each species, 60 undamaged intact crab specimens, 30 females and 30 males, were used for the study. The carapace width of each crab was measured with a pair of digital Vernier calipers. The entire second right maxilliped was carefully removed using a pair of fine forceps and mounted on a glass slide with a few drops of 70% glycerol. The inner surface of the second maxilliped was chosen to be studied as it is involved in the washing and sorting of sediment particles brought to the buccal cavity (see Miller 1961). As setation on the right and left maxilliped of the crabs are not expected to differ, only the right maxilliped was used for the study. Two types of setae—ST setae and P setae—were counted three times for each maxilliped under a compound microscope (magnification: 200 ×), and the means of these triplicate counts were used for data analyses. The coverage of the maxilliped surfaces by the two types of setae was estimated using the length of the maxilliped covered by the respective setae (see square brackets denoting setal type in Fig. 1), similar to methods used in Icely and Jones (1978).

Sediment size analyses of the substrate collected from the Rodman shore where *Leptuca terpsichores* and *L. beebei* lived were conducted to test for sediment particle size differences between the two microhabitats. This was carried out using methods outlined in Buchanan (1984). Data obtained from dry and wet sieving was analysed using GRADISTAT (version 9.1). Mass of different grained sized sediments were entered into the programme. which calculated the percentage of grains that fell into each size fraction (see Blott and Pye 2001). Since *P. panamensis* lives and forages among stones and rocks at Punta Culebra, no sediment samples were collected for analysis.

Statistical analyses

An analysis of covariance (ANCOVA) was performed using a general linear model (GLM) with 'number of ST setae/P setae' as the response variable, 'sex' as the factor and 'carapace width' as the covariate for separate sexes in each of the three species to test for sexual dimorphism. If the slopes were not significantly different, then a test of intercepts was carried out. No test of intercept was carried out if the slopes differ significantly. If both the slopes and intercepts were not significantly different (*i.e.*, no evidence of sexual dimorphism), then data for both sexes of each species were combined for subsequent ANCOVA comparisons among the three species, with 'species' as the factor in the analysis.

RESULTS

The results from the sediment analyses indicated that habitats in which *L. terpsichores* and *L. beebei* live comprised 99.6% sand and 0.4% mud (mean diameter: 247 μm), and 97.9% sand and 2.1% mud (mean diameter: 194 μm), respectively. According to GRADISTAT, the habitat of *L. terpsichores* was classified as moderately sorted medium sand (grains with a moderate range of sizes; particle diameter range: 0.25–0.5 mm) while that of *L. beebei* was designated as moderately sorted fine sand (grains with a moderate range of sizes; particle diameter range: 125–250 μm). Thus, the habitat of *L. beebei* had smaller sand particle size than that of *L. terpsichores*.

Approximately 70% of the inner surface of the second maxilliped of *L. terpsichores* (Fig. 1a) was covered with ST setae while 30% was covered with P setae. In contrast, each of the two setal types occupied ca. half of the inner surface of the second maxilliped of *L. beebei* and *Petruca panamensis* (Fig. 1b and 1c). This observation was consistent across both sexes in each species.
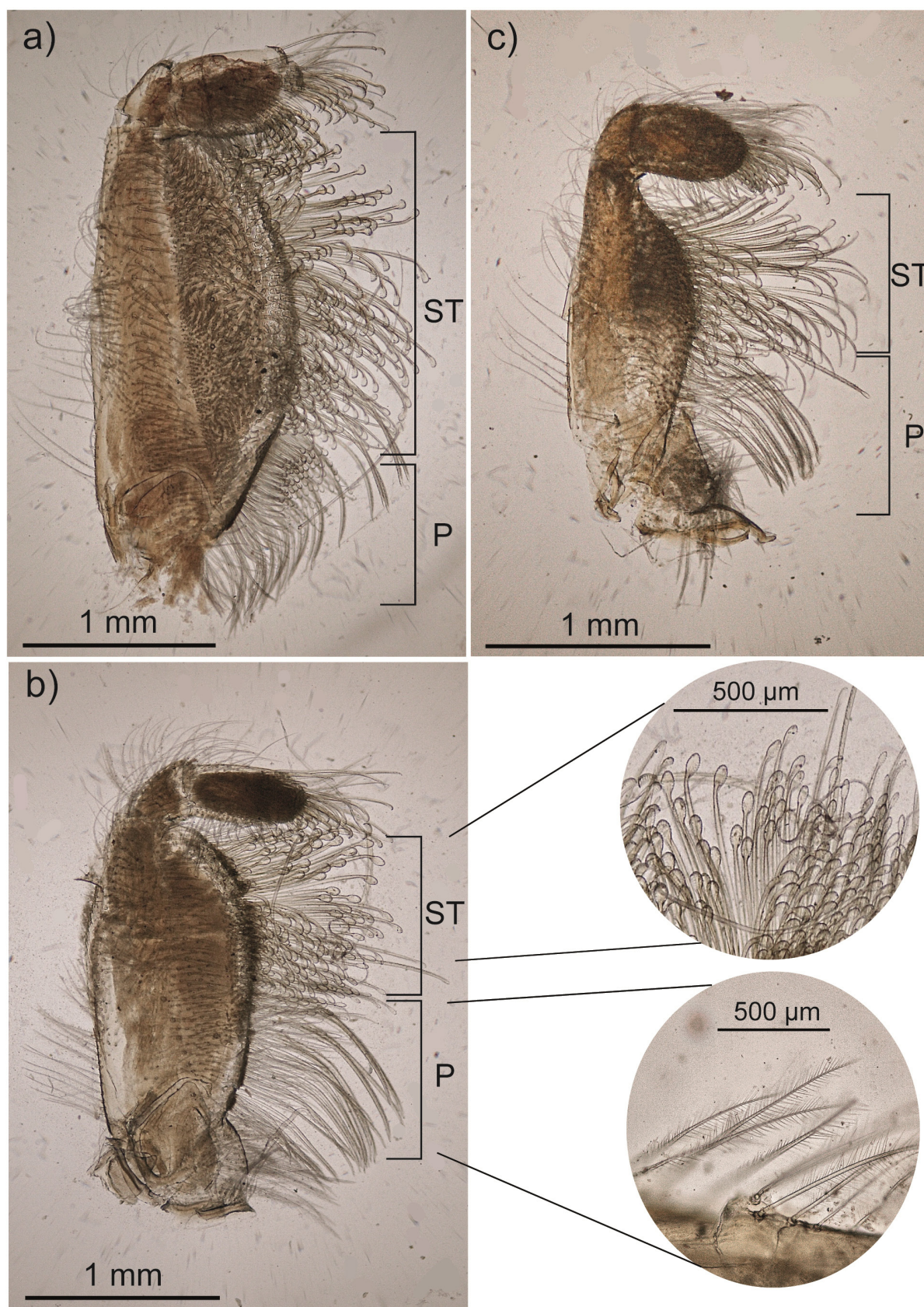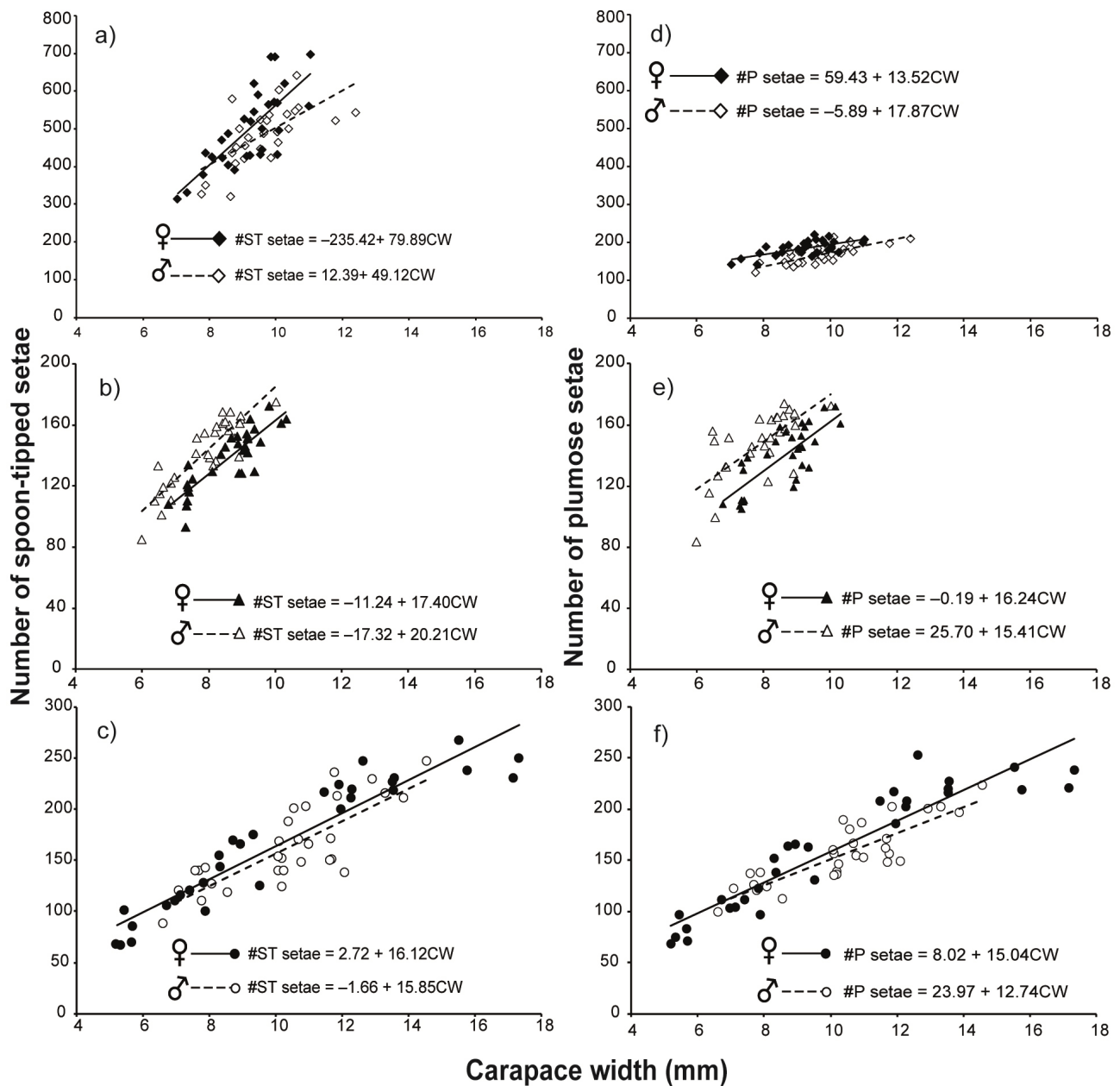
Fig. 1. Second maxilliped of: a) *Leptuca terpsichores*; b) *L. beebei*; c) *P. panamensis*. ST, spoon-tipped setae; P, plumose setae.

In all three species, the number of ST and P setae increased with increasing carapace width in males and females within the three species (Fig. 2). ANCOVA results showed that there were no significant differences ($p > 0.05$) between the slopes, nor between the intercepts of the regression equations of male and female crabs in all three species for ST setae, *i.e.*, there is no sexual dimorphism in the number of ST setae on the second maxillipeds. Similar results were observed for P setae, *i.e.*, there is no sexual dimorphism in the number of P setae as well. Hence, setation data for males and females within each species were combined to determine interspecific differences. All the regression equations for each species showed a positive linear relationship between the number of ST setae/P setae and carapace width (Table 1), indicating that the number of ST and P setae generally increased with increasing carapace width in all three species.

Fig. 2. Scatterplots and fitted regression lines of 'number of spoon-tipped setae' (a–c), and 'number of plumose setae' (d–f) against carapace width on the second maxilliped of a) *Leptuca terpsichores*: ◆ female, ◇ male (r^2 ♀ 0.57; r^2 ♂ 0.44); b) *L. beebei*: ▲ female, △ male (r^2 ♀ 0.74; r^2 ♂ 0.78); c) *Petruca panamensis*: ● female, ○ male (r^2 ♀ 0.88; r^2 ♂ 0.64); d) *L. terpsichores*: ◆ female, ◇ male (r^2 ♀ 0.45; r^2 ♂ 0.60); e) *L. beebei*: ▲ female, △ male (r^2 ♀ 0.61; r^2 ♂ 0.50); f) *P. panamensis*: ● female, ○ male (r^2 ♀ 0.87; r^2 ♂ 0.72).

When ST setation was compared across the three species, ANCOVA results showed that the slopes of at least one of the three regression lines was significantly different from the others (Table 2a, Fig. 3a). Tukey's test confirmed that for any given size of crab, the number of ST setae in *L. terpsichores* was significantly more than that of *L. beebei* and *P. panamensis*, while there was no significant difference between *L. beebei* and *P. panamensis*. In contrast, ANCOVA results on P setae data showed that there was no significant difference in the slopes as well as the intercepts of the regression equations for the three species ($p > 0.05$, Table 2b, Fig.

3b); indicating that for any given size of crabs, there is no difference in the abundance of P setae on the second maxilliped.

DISCUSSION

In a comprehensive account of the cumulative work carried out on the ecomorphological importance of maxilliped setae in fiddler crabs, Lim and Kalpana (2011) highlighted that other than Weissburg's (1991) observation that females of *Uca pugnax* had
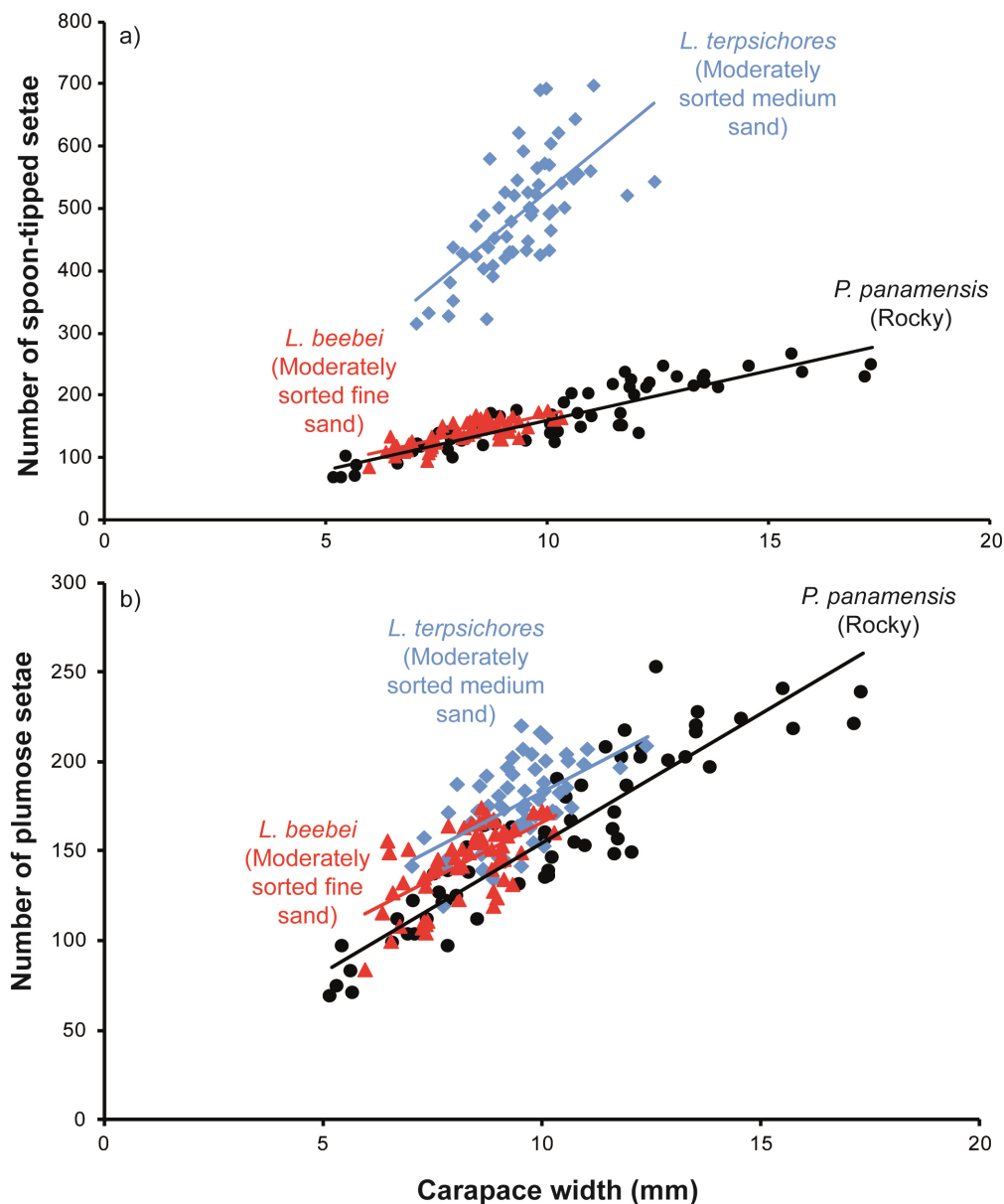
Fig. 3. Scatterplots and fitted regression lines of a) 'number of spoon-tipped setae' against carapace width and b) 'number of plumose setae' against carapace width on the second maxilliped of: ◆ *Leptuca terpsichores*, ▲ *L. beebei*, and ● *Petruca panamensis*.

10% to 15% more ST setae on their first and second maxillipeds, no other studies reported any similar sexual dimorphism trends. To date, quantitative data—based on enumeration of all the ST setae on the second maxillipeds of males and females, with size as covariate—are available for nine species (inclusive of *L. terpsichores*, *L. beebei* and *P. panamensis* in the present study). Furthermore, these nine species of fiddler crabs were from different geographical regions of the world, viz., Asia (see Yamaguchi and Ogata 2000; Lim 2004; Yamaguchi et al. 2005), Oceania (see Lim and Kalpana 2011) and Central America (current study), suggesting that the absence of sexual dimorphism where ST setation is concerned is general and widespread. Hence, the apparent sexual dimorphism as reported by Weissburg is most likely an artifact due to his use of small grids (ranging from 10×20 μm to 10×40 μm) that were randomly placed on various parts of the maxillipeds as an estimate of setal counts. Furthermore, more evidence is now available on the strategies that male fiddler crabs possess to compensate for the seeming disadvantage of foraging with one cheliped. For example, Yamaguchi et al. (2005) documented that although female *Uca arcuata* scoop 70% more frequently than males (due to using two chelipeds for feeding), males collect 46% more substratum per scoop than females. Similarly, Lim and Kalpana (2011) reported that male fiddler crabs can compensate for their foraging handicap by having longer or deeper minor chelipeds (*Uca perplexa* and *U. vomeris*, respectively) which enable them to scoop larger amounts of sediments. Hence, Weissburg's argument—that it is logical for females to have more ST setae to process larger quantities of sediment brought to the buccal cavity by two chelipeds—is tenuous, without due comparison with the morphometrics of the male conspecific's minor cheliped.

Crane (1975) provided some illustrations of ST setation on the second maxilliped of five fiddler crab species (p 355) and stated in her tome that the normal habitat of a given species, whether sandier or muddier, may be surmised merely by the examination of the setae: the more spoon-tips, the sandier the environment. Indeed, through the sketches by Icely and Jones (1978) in their study of four species of fiddler crabs from East African shores, with habitat characteristics, it can be estimated (from their diagrams) that 80% ST coverage

Table 1. Regression equations for 'number of spoon-tipped setae' and 'number of plumose setae' against 'carapace width' of *Leptuca terpsichores*, *L. beebei* and *Petruca panamensis*. #ST setae: number of spoon-tipped setae on second maxilliped; #P setae: number of plumose setae on second maxilliped; CW: carapace width

Species	*n*	Regression equation	r^2
Leptuca terpsichores	60	#ST setae = –62.40 + 58.92CW	0.447
	60	#P setae = 52.90 + 12.98CW	0.327
L. beebei	60	#ST setae = 8.10 + 16.03CW	0.615
	60	#P setae = 38.80 + 12.67CW	0.382
Petruca panamensis	60	#ST setae = 0.40 + 16.00CW	0.808
	60	#P setae = 10.25 + 14.44CW	0.827

Table 2. ANCOVA results the test of slopes and intercepts of regression equations of three species of fiddler crabs (*Leptuca terpsichores*, *L. beebei* and *Petruca panamensis*): a) Spoon-tipped setae against carapace width; b) Plumose setae against carapace width. *: significant; n.s.: not significant

Predictor	F	*p*	
a) Spoon-tipped setae			
Carapace width	138.88	0.000	
Species	0.72	0.487	
Carapace width × Species	29.19	0.000	*: Slopes significantly different
b) Plumose setae			
Carapace width	136.61	0.000	
Species	2.15	0.119	n.s.: Intercepts not different
Carapace width × Species	0.38	0.685	n.s.: Slopes not different

in *Uca lactea* (from a sandy habitat, mean grain size: 185 μm) was markedly more than the 20% observed in *U. chlorophthalmus* (from a soft, muddy habitat, mean grain size: 137 μm); the other two species, *U. tetragonon* and *U. vocans*, had ca. 50% and 40% ST setae coverage and mean grain size of 170 μm and 164 μm, respectively. Although Icely and Jones (1978) did not conduct a GRADISTAT analysis to characterize the sediment, the size ranges provided in their paper suggested that the sediments were mainly medium sand (for *U. lactea*) and fine sand for the other three species. It is pertinent to note that the authors described the habitat from which they collected *U. chlorophthalmus* as soft, rich mud, whereas Crane (1975) stated that this species' typical biotope is muddy sand. In this present study, the two congeneric species live in habitats that comprise mainly sand, differing only on the size range of the sand particles, *i.e.*, medium sand vs. fine sand. From visual examination of the second maxillipeds alone (see Fig. 1) it is evident—even without enumeration of the ST setae—that *L. terpsichores* has more ST setae than its congener, *L. beebei*.

Petruca panamensis has similar coverage proportions of the two different types of setae as that in *L. beebei*, suggesting that the sediment that accumulates on the surface of rocks is mainly fine sand. It is unfortunate that no sediment was collected or scraped off the rocks for comparisons with sediment from the *L. beebei* habitat because we would decimate the rocky habitat in which *P. panamensis* lives. When Takeda and Murai (2003) studied the feeding behavior of large, non-ovigerous female *P. panamensis* on rocky and sandy substrata at Punta Culebra, they observed two distinct behaviors: the crabs that fed on sandy substrates behaved like typical fiddler crabs that inhabit sandy habitats whereby small amounts of sand were scooped into the buccal cavity, sorted and ejected as pseudofecal pellets, whereas those on rocks directly swallow food materials pinched from the rock surfaces without sorting or production of pseudofecal pellets. The latter behavior was suggested to be a means of reducing loss of stored water by not ejecting wet pseudofecal pellets. Perhaps, this unique feeding method could be the reason as to why ST setae are present in smaller numbers.

When the absolute numbers of the ST setae were used for comparisons and corrected for maxilliped size (through ANCOVA with CW as the covariate), the results are unequivocal that both *L. beebei* and *P. panamensis* have significantly fewer ST setae than *L. terpsichores*. It is pertinent to note that the two congeneric species inhabit coastal habitats that are typical of fiddler crab biotopes—generally ranges from sandy to muddy sediment composition—while *P. panamensis* is unique in that the species lives among

rocks. Yet, through comparison of the abundance of ST setae, it is possible to discern that *L. terpsichores* comes from a sandy habitat that has larger sand grain size than *L. beebei* and has significantly more of this type of setae in the second maxilliped to cope with the sorting of larger sediment grains.

To date, most of the comparative work on the adaptations of fiddler crab mouthpart setation has been focused on ST setae, although there is a general belief that P setae abundance follows a reverse trend, as P setae are associated with muddier habitats. Scant information is available on the ecomorphological adaptation role played by P setae—be it comparisons between sexes within a species or interspecific comparisons—save for some brief mention of either coverage (*e.g.*, see Icely and Jones 1978; Checon and Costa 2017) or presence/absence (*e.g.*, see Thurman et al. 2013) of the P setae on the second maxilliped. Results of this present study as well as those of Lim and Kalpana (2011), however, show without a doubt that there is no sexual dimorphism in P setation in the five species of fiddler crabs studied, viz. *Leptuca terpsichores*, *L. beebei*, *Petruca panamensis*, *Uca perplexa*, and *U. vomeris*. In addition, both studies showed that there was no evidence of interspecific differences between and among fiddler crab species from habitats that differ in sediment particle size composition. This suggests that the functional significance of P setae for processing muddier sediments, as previously touted, is still debatable.

Checon and Costa (2017) did a broad grouping of fiddler crab species based on the presence of the dominant maxilliped setae: (a) plumose; (b) spoon-tipped; or (c) mixed. *Uca maracoani* and *U. thayeri* were classified as having a dominance of P setae, while *U. leptodactyla* was the only species having primarily ST setae. Four other species (*i.e.*, *U. burgersi*, *U. cumulanta*, *U. rapax* and *U. uruguayensis*) were deemed as having mixed setal types in various proportions. It is pertinent to note that 'dominance' was not defined in their study by any quantitative methods and there was no mention of the percentage coverage that constitutes this classification. Results from their multivariate analyses showed that sediment grain size, together with the presence of vegetation were the most important variables that accounted for fiddler crab distribution. They also cautioned against the prediction of potential distribution by mouthpart adaptations alone. While our results do indicate a positive relationship between sand grain size with the abundance of ST setae, we are, by no means, implying that distribution of the species can be inferred by this attribute alone.

As Thurman et al. (2013) alluded, the relationship between mouthparts and substrate may be flexible.

Their argument was based on Vernberg and Vernberg's (1967) observation that *U. uruguayensis* shows considerable feeding plasticity in the presence of congeners. More recently, Sayão-Aguiar et al. (2012) reported that when interspecific competition is low, *U. uruguayensis* occupies diverse habitats; but when congeners are present, it will select a narrower range of habitat characteristics whereby it can feed with greater efficiency. Hence, mouthpart adaptations seem to facilitate survival by allowing specialization under increased competitive pressure. All three species in this study had mixed setal types on their maxillipeds. This could be an indication that the three species may have the potential for feeding plasticity as well, especially when their preferred habitats are threatened. Takeda and Murai (2003) observed that *P. panamensis* preferred to feed on rocks rather than on sand. They considered that this fiddler crab species—through the morphological alteration of their minor chelipeds (with profuse tufts of setae), together with the ability to drain branchial chamber water onto rocks and to swallow food material without sorting—changed its habitat from sandy/muddy shores to the rocky shore. The fact that *P. panamensis* has ca. 50% coverage of ST on the second maxillipeds has enabled the species to feed on sandy substrates, when the sorting of ingested sediments is necessary, thereby showing plasticity in feeding behavior. However, until more species transplantation studies and/or substrate preference experiments are conducted with other species of fiddler crabs, we can only conclude at this juncture that mixed setation on the maxillipeds renders a greater potential for feeding plasticity.

CONCLUSIONS

Our results showed unequivocally that maxilliped setation in fiddler crabs is not sexually dimorphic. Differentiation of habitats down to the level of different sand-grain size, i.e., medium sand versus fine sand habitats of *L. terpsichores* and *L. beebei* is possible by using the abundance of ST setae as an indicator. Both *L. beebei* and *P. panamensis* had significantly fewer ST setae than *L. terpsichores*, possibly because the former two species' habitats have sediments with sand grains that are less coarse than the latter's. The significance of ST setae as an ecomorphological adaptation for efficient food extraction from sandy sediments is, thus, evident in *L. terpsichores*. As *P. panamensis* can directly swallow food materials pinched from the rock surfaces without sorting—a behavior suggested to reduce loss of stored water by not ejecting wet pseudofecal pellets—the role of the ST setae may be of secondary importance. The three species did not differ significantly in P setae

abundance, suggesting that the adaptive function of this type of setae to habitat characteristics, remains debatable. All three species in this study have both ST and P setae, albeit at different proportions. This may provide the possibility for potential feeding plasticity when preferred habitats are scarce.

Authors' contributions: Collected field specimens, conceived, and designed the study, analyzed the data as well as wrote the paper: SSLL; Performed all the laboratory work and some of the data analyses: SJAG.

Competing interests: The authors declare that they have no competing interests.

Availability of data and materials: The data generated and analyzed during the current study are available from the corresponding author.

Consent for publication: Not applicable.

Ethics approval consent to participate: We thank the ARAP for access to the study sites and the research permit for collection of crab specimens and sediment samples.

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