

Fiddler crab (*Brachyura: Ocypodidae*) inventory from the Parita Gulf, Panama

Inventario de los Cangrejos Violinista (*Brachyura: Ocypodidae*) en el Golfo de Parita, Panamá

Roberto C. Lombardo González

Universidad de Panamá, Departamento de Biología Marina.
Sistema Nacional de Investigación, Secretaría Nacional de Ciencia, Tecnología e Innovación, Panamá.

roberto.lombardo@up.ac.pa

<https://orcid.org/0000-0002-0279-8621>

Recibido
30/09/2024

Aceptado
25/01/2024

DOI <https://doi.org/10.48204/j.scientia.v35n1.a6621>

Abstract

We present the most recent inventory of fiddler crabs for the Gulf of Parita, covering both ecological and tourist sites of interest. Six sites in the gulf were sampled, where 22 species were identified. The most represented genus was *Leptuca* with 12 species. The inventory includes the new report of *Leptuca tallanica*, increasing the total number of fiddler crab species in the Panamanian Pacific to 32 and to 39 for the country.

Keywords: Carapace, crab, chela, distribution range, Eastern Pacific.

Resumen

Presentamos el inventario más reciente de cangrejos violinistas para el Golfo de Parita en sitios de interés ecológico y turístico. Se muestrearon seis sitios en el golfo, donde se determinaron 22 especies. El género mejor representado fue *Leptuca* con 12 especies. El inventario incluye el nuevo reporte de *Leptuca tallanica*, con lo cual se aumenta el número total de especies de cangrejo violinista en el Pacífico panameño a 32 y 39 para el país.

Palabras claves: Cangrejo, caparazón, Pacífico Oriental, quela, rango de distribución.

Introduction

Fiddler crabs are a typical component of the fauna inhabiting wetlands, mudflats, and mangroves worldwide (Crane, 1975). These crabs belong to the family Ocypodidae and have been the focus of numerous studies on behavior and ecology (Christy, 1987b, 1987a; Christy & Salmon, 1984; Christy & Wada, 2015; Crane, 1966; Kim & Christy, 2015). However, little is known about them in Panama, where most studies have been concentrated in the Panama Canal area (Lombardo, 2023). Fiddler crabs are distinguished by a notable sexual dimorphism: males possess hypertrophied claws with disproportionately robust and elongated manus and dactyls, in contrast to females (Crane, 1975; von Hagen, 1968).

Of the 107 species recognized on the “Fiddler Crabs” website (<http://www.fiddlercrab.info/index.html>) (Rosenberg, 2001, 2014, 2019), 38 are associated with marine-coastal ecosystems in Panama (Crane, 1975; Lombardo, 2022, 2024; Rosenberg, 2019). In Panama’s Pacific region, four genera are recognized: sixteen species belong to *Leptuca*, six to *Uca*, and eight to *Minuca*, along with *Petruca panamensis*, recently reclassified in the genus *Petruca* (Rosenberg, 2014, 2020; Shih et al., 2016; Shih et al., 2015). Some species exhibit cryptic characteristics, such as small size or indistinct coloration, complicating their detection (Crane, 1975; Hendrickx, 1979). This is concerning given the vast variability of coastal-marine landscapes and the changes they are undergoing due to environmental degradation (Lourie & Vincent, 2004) and climate change (Kwiecinski & D’Croz, 2008).

In this context, two possible explanations arise: (1) the presence or absence of species may have changed, or (2) previously unrecorded species may now be present without formal documentation. For this reason, an updated inventory could clarify the presence and distribution ranges of these species, providing a basis for future environmental impact assessments (Silveira et al., 2010).

Since the work of Rathbun (1902) and Crane (1941), reports on fiddler crabs in the Eastern Pacific province have established the presence and distribution of multiple species from Mexico to Peru (Beinlich & von Hagen, 2006; Crane, 1975; Hendrickx, 1979, 1995b, 1995a; Hendrickx & Salgado-Barragán, 1992; Landstorfer & Schubart, 2010; Lazarus & Cantera, 2007; Rathbun, 1902, 1904, 1935; Rosenberg, 2014, 2020; von Hagen, 1968). Recent studies report two new species for Panama: *Minuca osa* (Lombardo, 2022) and *Minuca zaca* (Lombardo, 2024). These discoveries underscore the importance of inventories, which are essential for decision-making in activities that affect biodiversity (Silveira et al., 2010). However, no recent inventories of fiddler crabs exist in Panama, complicating assessments of their population status.

Although fiddler crabs are not part of economically significant fisheries, they play essential ecological roles. They are considered ecosystem engineers (Aschenbroich et al., 2016; Kristensen, 2008) and are critical in energy flow, linking lower and upper trophic levels in mangrove ecosystems (Lindquist et al., 2009; Smith et al., 1991). As primary consumers, they are part of the diet of numerous avian predators (Lombardo González, 2023), making their populations vital for migratory birds. This recognition has been granted by the municipality of Chitré and the Western Hemisphere Shorebird Reserve Network Council (MiAmbiente, 2024).

Furthermore, the burrowing activity of fiddler crabs mixes sediment, increasing oxygen contact (bioturbation), which influences various physicochemical processes (Agusto et al., 2021; Aschenbroich et al., 2016; Booth et al., 2019; Kristensen, 2008). For example, they impact plant recruitment by influencing the distribution of organic carbon in the soil and reducing the salinity of interstitial water (Agusto et al., 2021; Aschenbroich et al., 2016; Griffiths et al., 2007; Lindquist et al., 2009). The environmental services generated by their activity are crucial to the functioning of mangroves, ecosystems internationally recognized for their value to

humanity (Cámara et al., 2004).

Fiddler crabs also have great potential as bioindicators, having been successfully used to detect trace elements and other contaminants (Bartolini et al., 2009; Lavezzo et al., 2020), as well as to assess the impact of human activity in coastal areas (Gül & Griffen, 2019). An updated inventory of fiddler crabs in the Gulf of Parita would allow for monitoring ecosystem conditions and aid in the planning of management measures. Therefore, the objective of this study was to identify the fiddler crab species in ecological and touristic sites of interest within the Gulf of Parita, Panama, Pacific.

Methods

Study site

The Gulf of Parita has a tropical savanna climate (Aw) according to the Köppen climate classification (Beck et al., 2018). Annual temperatures range between 24°C and 30°C, with minimal seasonal variation. The rainy season extends from May to November, characterized by abundant rainfall, especially in October (1,500 to 2,500 mm), and a dry season from December to April, with reduced precipitation. Relative humidity is high during the rainy season, frequently exceeding 80%, while during the dry season it decreases but remains around 60-70% (Instituto de Meteorología e Hidrología de Panamá, 2024).

The gulf includes approximately 15,000 hectares of intertidal mudflats, extending from the South of Antón, in the province of Coclé in the northeast, to the La Villa River, in the provinces of Los Santos and Herrera in the southwest. The Gulf includes three protected areas: the Cenegón del Mangle Wildlife Refuge, the Sarigua National Park, and the Peñón de la Honda Wildlife Refuge. Six rivers flow into Parita Bay: Hondo River, Grande River, Pocrí River, Santa María River, Parita River, and

La Villa River (Instituto Geográfico Nacional Tommy Guardia, 1988; MiAmbiente, 2024). This study focused on the sites El Salado de Aguadulce (SA), Playa El Retén (RE), Playa El Agallito (AG), Los Aromos (RO), Playa Las Comadres (CO), and Playa El Uverito (UV). The selection criteria include the diversity of habitats available for fiddler crabs, the importance of the sites for migratory birds, access, and tourist services (Figure 1).

Sampling and species identification

Twenty trips were conducted during 2024, distributed as follows: three to El Salado de Aguadulce (May 12 and 18, June 6), two to Playa El Retén (August 6 and 10), ten to Playa El Agallito (May 19 and 23, June 8, 9, 22, and 29, July 6, 7, and 21, September 2), three to an abandoned shrimp farm in Los Aromos (April 14, May 4 and 18), one to Playa Las Comadres, and one to Playa El Uverito (Figure 1). The sampling methodology consisted of two parts. The first was direct detection of crabs in different habitat types, primarily based on substrate type. For example, stable muddy substrates in mangrove forests, along estuary shores, and sandy-muddy substrates at river mouths on beaches (Backwell et al., 1998; Crane, 1941, 1975). The second part involved photographic documentation of individuals using a camera (Sony Alpha 5100) with macro lenses (Sony 30mm f/3.5) and telephoto lenses (Sony 55-210mm f/4.5-6.3; Tamron 50-400mm f/4.5-6.3). The goal of photography in natural conditions was to maintain a reference of the coloration of individuals, given its importance for identification. Once the image capture and behavioral observations in the field were completed, reference specimens were collected either by burrow excavation or by hand at the surface.

After collection, specimens were transported alive or, if necessary, preserved in 90% alcohol to the Biodiversity Training, Research, and Monitoring Center (CCIMBIO) for processing. The crabs were euthanized by cooling (-4°C) for ten minutes. Following this, the sex of the crabs was determined, and biometric variables

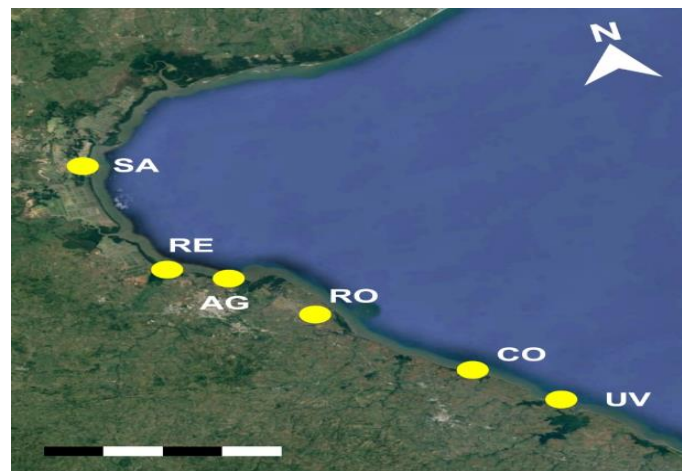
(using a caliper with 0.1 mm precision) such as carapace width (CW), chela height (QH), and chela length (QL) were recorded.

Detailed examination for species identification was carried out using specialized identification keys (Beinlich & von Hagen, 2006; Bott, 1954; Crane, 1941, 1975; Landstorfer & Schubart, 2010; Peters, 1955; Rathbun, 1902, 1904, 1935; Rosenberg, 2019; H. Te Shih et al., 2015, 2016; von Hagen, 1968; von Prael & Toro, 1985).

Additionally, the websites <https://www.fiddlercrab.info/index.html> (Rosenberg, 2014) and <https://www.inaturalist.org/journal/msr/82286-fiddler-crab-guide-pacific-coast-of-the-americas> (Rosenberg, 2023) were consulted for the identification of candidate species. Diagnostic structures were evaluated using a stereoscope (SZ2-ILST) equipped with a mounted digital camera (EP50) and EPview software (Olympus, Japan). Field images were processed for framing and resolution using the open-source program GIMP (ver. 2.10.36).

Figura 1.

Relative location of the sampling sites for fiddler crabs in the Gulf of Parita, Panama, Pacific. Sites include: El Salado de Aguadulce (SA), Playa El Retén (RE), Playa El Agallito (AG), Los Aromos (RO), Playa Las Comadres (CO), and Playa El Uverito (UV). Scale: 20 km.



Results

The presence of 22 species of fiddler crabs was determined, distributed differentially across the six sampling sites. The count includes the four genera reported for the Pacific. The best-represented genus was *Leptuca* with 12 species, followed by *Uca* with five, *Minuca* with four, and *Petruca panamensis* (Table 1). Regarding the genus *Leptuca*, the species *Leptuca tallanica* (von Hagen, 1968) is reported as new to the country (Lombardo, in press). This species increases the number of *Leptuca* species in the Panamanian Pacific to 17. Three species (*L. batuenta*, *L. inaequalis*, and *U. ornata*) were found exclusively at Playa El Agallito, while *Petruca panamensis* was collected only at El Salado.

Species identification

The identification of each species has been confirmed morphologically; however, to facilitate identification for the layman, the following annotated list is meant to aid species identification from field observations highlighting size, shape, structure, color variants and behavioral features which are of diagnostic value (see Annex for figures).

***Leptuca batuenta*:** It is among the smallest of all fiddler crabs (Table 1) and can go unnoticed due to its tiny size. However, it is easy to identify thanks to the distinctive shape of its major chela. Specifically, the pollex has a characteristic tooth pattern, where the pollex curves upward around three-quarters of its length to meet a tooth, then curves downward with a concave edge ending in a point. The claw is generally white, while the limbs tend to be a reddish-brown color (Figure 2). El Salvador to northern Peru.

***Leptuca oesterdi*:** It is distinguished by its unique aqua-blue coloration, which is often observed across the crab's entire front, although it is not always

present on the carapace or visible from the back. The major chela also has a characteristic shape, with a notch at the base of the pollex, followed by an almost straight edge that extends to the tip of the dactylus (Figure 3). El Salvador to Panamá.

Leptuca inaequalis: The major chela is a gray-brown tone, with a dark red/brown spot on the lower edge near the base of the pollex; the fingers are usually white, and an orange tint is often observed along the upper edge of the dactylus. The space between the fingers of the claw is almost always filled with mud due to small hairs on the proximal half of the pollex that trap the mud. The shape of the pollex is not markedly triangular like in *Leptuca saltitanta*, but it has a robust palm with short, thick fingers (Figure 4). El Salvador to northern Peru.

Leptuca tomentosa: Little-known but reasonably distinctive species. The upper edge of the distal section of the pollex on the major chela flattens into a straight edge leading to the tip. It has a marbled carapace in dark and light green tones, with yellow spots; green eye stalks; and a pale claw with light brown on the margins (Figure 5). El Salvador to northern Peru.

Leptuca tallanica: The identification of specimens at two sites in the Gulf of Parita was confirmed by the presence of a moderately wide front, comma-shaped hairy patches on the male carapace, a triangular hairy depression at the base of the pollex, and a strong tuberculate projection on the subdistal section of the pollex (Figure 6). Originally from southern Ecuador to northern Peru.

Leptuca umbratila: A particularly narrow front compared to other species in the *Leptuca* genus. Essentially, its front is only moderately wider than that of other *Uca* species, but without the narrow appearance between the eyes characteristic of those species (Figure 7). The major chela has yellowish to white fingers. Eye stalks are wine-red, and the anterolateral edges are straight and well-defined. El Salvador

to Colombia.

Leptuca festae: It can reach a larger size compared to other species in the *Leptuca* genus, growing up to 15 mm in carapace width. The major chela has disproportionately long fingers compared to other species in its genus (Figure 8). The coloration is generally dull brown or grayish-brown, sometimes almost black, with yellow eye stalks and slight discoloration on the major chela. The waving motion of males is circular, where the claw is raised high. El Salvador to Ecuador.

Leptuca beebei: It is very common in intertidal muddy flat sites. It structurally resembles *Leptuca stenodactylus*. It is more generalist in terms of mud or sand habitats compared to many of the other species described, and it can be confused with several of them. However, in the field, the carapace is often a mix of dull green, blue, or brown, the major chela is frequently a pale gray or white but has a dark purple spot at the base of the pollex, and its eye stalks tend to be yellow (Figure 9). El Salvador to northern Peru.

Leptuca stenodactylus: Similar in size and shape to *Leptuca terpsichores*, it is often found in sandier substrates, where the two species typically overlap. However, it stands out due to its bright coloration: a blue and white carapace, red legs, and a pink or white major chela (Figure 10). El Salvador to Chile.

Table 1

List of fiddler crab species at ecological and tourist sites in the Gulf of Parita, Panama, Pacific. The carapace width (CW) is the average observed. The substrate types include sandy (ARE), sandy-muddy (AFAN), stable mud (FAE), unstable mud (FAI), and rocky intertidal (IROC). The sampling sites are: Salado de Aguadulce (SA), Playa El Retén (RE), Playa El Agallito (AG), Los Aromos (RO), Playa Las Comadres (CO), and Playa El Uverito (UV).

Species	Authority	CW (mm)	Substrate	Sex	Locality
<i>Leptuca batuenta</i>	Crane, 1941	6.7	FAI	♂	AG
<i>Leptuca oesterdi</i>	Rathbun, 1904	11.2	AFAN, FAI	♂	AG, RE
<i>Leptuca inaequalis</i>	Rathbun, 1935	7.5	FAI	♂	AG
<i>Leptuca tomentosa</i>	Crane, 1941	15.3	AFAN, FAE	♂, ♀	SA, AG, RE
<i>Leptuca tallanica</i>	von Hagen, 1968	10.6	AFAN, FAE	♂, ♀	SA, AG
<i>Leptuca umbratila</i>	Crane, 1941	28.9	FAI	♂, ♀	AG, RE, RO, CO
<i>Leptuca festae</i>	Nobili, 1902	11.1	FAE	♂, ♀	AG, RE
<i>Leptuca beebei</i>	Crane, 1941	10.3	FAE	♂, ♀	SA, AG, RE
<i>Leptuca stenodactylus</i>	Milne-Edwards & Lucas, 1843	10.5	ARE, AFAN, FAI	♂, ♀	SA, AG, CO
<i>Leptuca deichmanni</i>	Rathbun, 1935	9.4	ARE, AFAN	♂	CO, UV, AG
<i>Leptuca terpsichores</i>	Crane, 1941	8.4	ARE	♂, ♀	AG, RE, CO
<i>Leptuca latimanus</i>	Rathbun, 1893	12.8	ARE, AFAN	♂, ♀	SA, RO, RE, AG
<i>Uca heteropleura</i>	Smith, 1870	18.9	AFAN, FAE	♂, ♀	SA, RE, AG
<i>Uca intermedia</i>	von Prael & Toro, 1985	12.7	AFAN, FAE	♂	RE, AG
<i>Uca ornata</i>	Smith, 1870	38.7	FAI	♂, ♀	AG
<i>Uca princeps</i>	Smith, 1870	38.3	FAI	♂	AG, RO
<i>Uca stylifera</i>	Milne-Edwards, 1852	21.8	AFAN, FAE	♂, ♀	SA, AG, CO
<i>Minuca argilicola</i>	Crane, 1941	10.6	FAE	♀	CO
<i>Minuca galapagensis</i>	Rathbun, 1902	21.8	FAE	♂, ♀	SA, RE, AG
<i>Minuca herradurensis</i>	Bott, 1954	22.4	AFAN, FAE	♂, ♀	SA, RE, RO
<i>Minuca zacaе</i>	Crane, 1941	10.7	FAE	♂, ♀	RO, RE
<i>Petruca panamensis</i>	Stimpson, 1859	13.5	ARE, IROC	♂, ♀	SA

***Leptuca deichmanni*:** The carapace is mottled in brown and gray tones, blending with the sandy surfaces where it typically inhabits. The front of the crab, around the mouth and eye orbits, is pale blue-gray (Figure 11B) to greenish in juveniles (Figure 11E). The exterior of the major chela is completely white, while the interior can show a mix of dark blues and reds. The tip of the pollex often has a slight concave curve. Like *L. terpsichores* and *L. stenodactylus*, it has a wider opening in

the minor chela compared to other species, such as *L. beebei*. Behavior helps differentiate *L. deichmanni* from other species, as its major chela movement is unique. *Leptuca deichmanni* performs a vertical up-and-down motion with its major chela, with a distinctive pause in the elevated position. Costa Rica to northern Colombia.

***Leptuca terpsichores*:** When males emerge from their burrows, they generally display a mottled brown-reddish color. However, within about 15 minutes, their color changes almost completely to white, except for a hint of pink or purple at the base of the major chela (Figure 12). This is the color observed most of the time. A more subtle trait is found in the minor chela: the opening between the fingers (Figure 12B) is notably large compared to most other species. Southern Guatemala to northern Peru.

***Leptuca latimanus*:** It appears to be a mix between *L. saltitanta* and *L. inaequalis*, although the pollex is not triangular and is somewhat larger. During courtship, its carapace is predominantly white (Figure 13C, D), with dark legs, and its major chela is a dark brown-red color with white tips on the fingers. The major chela has a particularly robust appearance, with a very wide palm and short, thick fingers. When shaking the chela, the inside of the arm may display shades of blue. During courtship, the movement of the major chela is accompanied by a seemingly circular motion of the minor chela in the direction of the lateral movement of the body in 2 or 3 steps. This species, like *L. terpsichores* and *L. beebei*, builds structures (semi-dome) next to the entrance of the burrow associated with courtship activity. Mexico to Ecuador.

***Uca heteropleura*:** In practice, it can be confused with some color variants of *U. princeps*. *Uca heteropleura* has a carapace and legs predominantly red to black (sometimes lightening to white or with slightly more purple tones), with the underside of the major chela red and the dactyl white. Its eye stalks are usually black with a

bright blue base (Figure 14A). The large chela tends to have relatively short and robust fingers, and its exterior surface is often notably rough. During courtship, the "greeting" movement of *U. heteropleura* is very different from that of *U. princeps*, allowing for easy differentiation in the field and even sometimes in photographs. Males of *U. heteropleura* perform their "greeting" by raising the major chela in front of them and elevating their entire body vertically on the tips of their legs, with the chela held above (Figure 14C, D). In contrast, *U. princeps* moves from side to side while keeping the chela extended laterally. El Salvador to northern Peru.

***Uca intermedia*:** It has only been recorded on the coasts of Panama and Colombia, and it appears to be a very rare species; it could only be observed at Playa El Agallito. Nevertheless, its identification in the field should be straightforward, as it is distinguished by being an almost entirely black fiddler crab, with a major chela that is yellow, orange, and red (Figure 15). Panama and Colombia.

***Uca ornata*:** The largest fiddler crabs, distinguishable from the rest by the shape of their major chela, are comparable only to the Atlantic species *U. maracoani*. The chela resembles pruning shears, with large, compressed fingers that meet at a very straight inner edge, while the upper edge of the pollex features a distinctive curvature (Figure 16). The carapace can vary from pale white (male in courtship, Figure 16A) or beige to darker tones of orange or reddish-purple, especially in females. When the crab is not covered in mud, the major chela is usually orange or dark yellow. Unfortunately, *U. ornata* and *U. insignis* (a sympatric species not observed) can be difficult to differentiate, as some distinguishing features are quite subtle. One detail that may help distinguish the males of both species is the mud pattern on the major chela of the crab. Typically, *U. ornata* is completely covered in mud, but even if most of the crab is "clean," the pollex of the major chela is almost never so. This is because the pollex has cavities filled with small hairs that hold onto the mud. This leaves males with a more or less permanent layer of mud on the

underside of the chela. In contrast, *U. insignis* has little hair on the exterior of its pollex, so it tends not to remain uncovered. El Salvador to northern Peru.

***Uca princeps*:** The most common colors in this species are pale yellow and orange, with some touches of white. The carapace of adults is usually reddish or yellow, sometimes lightening to white (Figure 17F). The ambulatory appendages tend to be more of an orange-yellow hue, while the major chela is generally a more intense orange, with the pollex and dactyl being white. The major chela of *U. princeps* typically features fingers that are longer than the palm, whereas in other species, the fingers are usually the same length or shorter than the palm. Southern California (USA) to Peru.

***Uca stylifera*:** Males of the species are easily distinguished by a long stylus that protrudes from the eye on the same side as the major chela; this stylus is approximately the same length as the rest of the ocular peduncle (Figure 18A, C-E). Although *U. intermedia* and *U. heteropleura* may have styluses, these are considerably shorter. Males have a carapace that varies from yellow to white, yellow eyes, orange-reddish to purple legs, and a major chela with an orange pollex and a white dactyl. Females of *U. stylifera* (Figure 18F) are somewhat more difficult to distinguish, as they lack the stylus and typically have a brown to dark purple coloration; they are more easily identified by their association with the males. El Salvador to northern Peru.

***Minuca argilicola*:** A little-known species, relatively small (~1 cm), predominantly beige with a slightly darker and shorter major chela. In the field, it is characterized by being very lethargic and inactive. Morphologically, the species has a rather generic appearance, somewhat similar in color to *M. galapagensis*, although the latter can reach larger sizes with a longer major chela. In this inventory, only the female of the species was observed at a single site, in the mangroves at the mouth of a creek in Playa Las Comadres (Figure 19). Costa Rica to Colombia.

Minuca galapagensis: A species with color polymorphism in at least three variants, two of which are reported in this inventory: the white variant (Figure 20) and the red variant (Figure 21). The olive-green variant with a yellow major chela was not observed. *Minuca galapagensis* appears to be one of the few species in the genus that is predominantly white. The "canonical" coloration of this species is mostly white to light beige, with a more intense yellow major chela, sometimes orange or red. Some individuals may be a more muted brown, orange, or a mix, complicating their identification, as they begin to resemble other *Minuca* species closely. Costa Rica to Ecuador; Galápagos Islands.

Minuca herradurensis: It is similar to *M. galapagensis*, but lacks the striking white color, instead showing a more "pale cream" tone and without a red morphotype. The carapace is gray or beige, with a major chela that is light brown or gray, with orange, yellow, or pink hues, and the distal half of the pollex is white. The upper surface of the manus of the major chela is usually covered with visible tubercles, while the underside has a noticeably smoother appearance (Figure 22). El Salvador to Panamá.

Minuca zaca: This is a small species (~1 cm) with a thick chela and relatively short fingers. Its carapace has a black base, with shiny gold and copper streaks and spots (Figure 23B), while the chela varies from a red-brown to an orange-pink hue, with white-tipped fingers. It is similar to *Leptuca pygmaea*, a species not observed in this inventory; however, the size and shape of the chela should be sufficient to differentiate them in the field. Originally, Mexico to Costa Rica.

Petruca panamensis: The only species of fiddler crab in the world that predominantly lives in rocky intertidal zones. Its carapace is flatter than in other species, and its major chela is notably smooth, lacking many armor details or teeth. It generally exhibits solid colors, usually light or dark gray. The major chela is often

beige, with a white pollex; however, the upper edge of the pollex is noticeably darker than the rest of the finger. El Salvador to northern Peru.

Among the species reported for the Panamanian Pacific but not observed in the present inventory are: *Leptuca dorotheae*, *Leptuca limicola*, *Leptuca pygmaea*, *Leptuca saltitanta*, *Leptuca tenuipedis*, *Minuca brevifrons*, *Minuca ecuadoriensis*, *Minuca osa*, and *Uca insignis*.

Discussion

Of the 107 species listed on the "Fiddler Crabs" website (<http://www.fiddlercrab.info/index.html>) (Rosenberg, 2014, 2019), 38 are associated with marine-coastal ecosystems in Panama (Crane, 1975; Lombardo, 2022; Shih et al., 2016). In the Caribbean, seven species are identified across three genera: four from the genus *Minuca*, two from the genus *Uca*, and *Leptuca thayeri*. In the Panamanian Pacific, four genera are recognized, with sixteen species from the genus *Leptuca*, six from the genus *Uca*, and eight from the genus *Minuca*, in addition to *Petruca panamensis*, which has been reclassified into the new genus *Petruca* (Rosenberg, 2014, 2020; Shih et al., 2015). However, this work includes the report of *Leptuca tallanica* (in press), another new species of fiddler crab for Panama, originally described in Puerto Pizarro, Peru (von Hagen, 1968) and in Puerto Bolívar, Ecuador (Crane, 1975). This tally updates the total number of fiddler crab species to 32 for the Pacific and 39 for the country. This overview suggests that, due to the scarcity of studies and the potential to employ phylogenetic techniques, the number of species could increase in the coming years.

The species reported for the region that could not be observed consist of a group of taxonomically difficult species to identify without detailed morphological analysis and others that are uncommon. In this scenario, the distribution of fiddler crab species largely depends on salinity and substrate type (Arruda et al., 2006;

Mokhtari et al., 2015; Peer et al., 2018; Thurman et al., 2013). For example, in our sampling sites, there were no tall mangrove areas and stabilized sandy-mud sediments, which are usually dominated by species of the genus *Minuca* (Crane, 1975; Lombardo, 2022). Likewise, *P. panamensis* is only found on rocky substrates. Only in El Salado was a segment of rocky intertidal observed in proximity to a mudflat and mangrove edge, which is why it was not seen at the other sampling sites. Although determining differences in diversity between sites was not our objective, habitat availability may have been an important factor in the results of our inventory, as there are fiddler crabs highly specialized to different physical characteristics of the environment (Peer et al., 2018; Thurman et al., 2013).

This study highlights the importance of comprehensive inventories to update lists and clarify the distribution ranges of fiddler crab species, which is fundamental to guiding future biodiversity conservation efforts (Silveira et al., 2010).

Conclusion

The presence of 22 species of fiddler crabs was determined. The count includes the four genera (*Leptuca*, *Minuca*, *Uca*, and *Petruca*) reported for the Eastern Pacific Realm. The best-represented genus was *Leptuca*, with 12 species.

Acknowledgements

We thank Carl Thurman, Hsi-Te Shih, John Christy, and Michael Rosenberg for preliminarily evaluating the images of specimens, the anonymous reviewers for their comments on the manuscript, and Virgilio Villalaz for directions to the site at Los Aromos.

Bibliographical References

- Agusto, L. E., Fratini, S., Jimenez, P. J., Quadros, A., & Cannicci, S. (2021). Structural characteristics of crab burrows in Hong Kong mangrove forests and their role in ecosystem engineering. *Estuarine, Coastal and Shelf Science*, 248. <https://doi.org/10.1016/j.ecss.2020.106973>
- Arruda, L. E., Braga, C., Ximenes, G., & Matthews-Cascon, H. (2006). Spatial distribution of fiddler crabs (genus *Uca*) in a tropical mangrove of northeast Brazil. *Scientia Marina*, 70(4), 759–766. <https://doi.org/10.3989/scimar.2006.70n4759>
- Aschenbroich, A., Michaud, E., Stieglitz, T., Fromard, F., Gardel, A., Tavares, M., & Thouzeau, G. (2016). Brachyuran crab community structure and associated sediment reworking activities in pioneer and young mangroves of French Guiana, South America. *Estuarine, Coastal and Shelf Science*, 182, 60–71. <https://doi.org/10.1016/J.ECSS.2016.09.003>
- Backwell, P. R. Y., O'Hara, P. D., & Christy, J. H. (1998). Prey availability and selective foraging in shorebirds. *Animal Behaviour*, 55(6), 1659–1667. <https://doi.org/10.1006/anbe.1997.0713>
- Bartolini, F., Penha-Lopes, G., Limbu, S., Paula, J., & Cannicci, S. (2009). Behavioural responses of the mangrove fiddler crabs (*Uca annulipes* and *U. inversa*) to urban sewage loadings: Results of a mesocosm approach. *Marine Pollution Bulletin*, 58(12), 1860–1867. <https://doi.org/10.1016/J.MARPOLBUL.2009.07.019>
- Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A., & Wood, E. F. (2018). Present and future köppen-geiger climate classification maps at 1-km resolution. *Scientific Data*, 5. <https://doi.org/10.1038/sdata.2018.214>
- Beinlich, B., & von Hagen, H. O. (2006). Materials for a more stable subdivision of the genus *Uca* Leach. *Zoologische Mededelingen*, 80(4), 9–32. <http://www.repository.naturalis.nl/document/41396>
- Booth, J. M., Fusi, M., Marasco, R., Mbobo, T., & Daffonchio, D. (2019). Fiddler crab bioturbation determines consistent changes in bacterial communities across contrasting environmental conditions. *Scientific Reports*, 9(1), 1–12. <https://doi.org/10.1038/s41598-019-40315-0>
- Bott, R. (1954). Dekapoden (Crustacea) aus El Salvador. 1. Winkerkrabben (*Uca*). *Senckenbergiana Biologica*, 36(3/4), 155–180.
- Cámara, R., Díaz del Olmo, F., Martínez, J. R., Morón, M., Gómez-Ponce, C.,

- Tabares.E., & Vega, A. (2004). *Directrices de gestión para la conservación y desarrollo integral de un humedal centroamericano: Golfo de Montijo (litoral del Pacífico, Panamá)*.
- Christy, J. H. (1987a). Competitive mating, mate choice and mating associations of brachyuran crabs. *Bulletin of Marine Science*, 41(2), 177–191.
- Christy, J. H. (1987b). Female choice and the breeding behavior of the fiddler crab *Uca beebei*. *Journal of Crustacean Biology*, 7(4), 624–635.
- Christy, J. H., & Salmon, M. (1984). Ecology and evolution of mating systems of fiddler crabs (Genus *Uca*). *Biological Reviews*, 59(4), 483–509. <https://doi.org/10.1111/J.1469-185X.1984.TB00412.X>
- Christy, J. H., & Wada, K. (2015). Social ethology in Brachyura. In P. Castro, P. Davie, D. Guinot, F. Schram, & C. von Vaupel Klein (Eds.), *Treatise on Zoology - Anatomy, Taxonomy, Biology. The Crustacea, Volume 9 Part C* (Vol. 9, pp. 417–468). BRILL. https://doi.org/10.1163/9789004190832_010
- Crane, J. (1941). Eastern Pacific expeditions of the New York Zoological Society. XXVI. Crabs of the genus *Uca* from the west coast of Central America. *Zoologica; Scientific Contributions of the New York Zoological Society*, 26, 145–208.
- Crane, J. (1966). Combat, display and ritualization in Fiddler Crabs (Ocypodidae, genus *Uca*). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 251(772), 459–472. <https://doi.org/10.1098/rstb.1966.0035>
- Crane, J. (1975). Fiddler crabs of the world: Ocypodidae: Genus *Uca*. In *Fiddler Crabs of the World: Ocypodidae: Genus Uca* (1st ed.). Princeton University Press. <https://doi.org/https://doi.org/10.1515/9781400867936>
- Griffiths, M. E., Mohammad, B. A., & Vega, A. (2007). Dry season distribution of land crabs, *Gecarcinus quadratus* (Crustacea: Gecarcinidae), in Corcovado National Park, Costa Rica. *International Journal of Tropical Biology and Conservation*, 55(1), 219–224.
- Gül, M. R., & Griffen, B. D. (2019). Burrowing behavior and burrowing energetics of a bioindicator under human disturbance. *Ecology and Evolution*, 9(24), 14205. <https://doi.org/10.1002/ECE3.5853>
- Hendrickx, M. E. (1979). Range extensions of fiddler crabs (Decapoda, Brachyura, Ocypodidae) on the Pacific coast of America. *Crustaceana*, 36(2), 200–202. <https://doi.org/10.1163/156854079X00447>

- Hendrickx, M. E. (1995a). Cangrejos. In Guía FAO para la identificación de especies para los fines de la pesca: Pacífico Centro-Oriental. (1st ed., Vol. 1, pp. 581–636). FAO. 646.
- Hendrickx, M. E. (1995b). Checklist of brachyuran crabs (Crustacea: Decapoda) from the eastern tropical Pacific. *Bulletin de L'institut Royal Des Sciences Naturelles de Belgique*, 65, 125–150.
- Hendrickx, M. E., & Salgado-Barragán, J. (1992). New records of two species of brachyuran crabs (Decapoda: Brachyura) from tropical coastal lagoons, Pacific coast of Mexico. *Revista de Biología Tropical*, 40(1), 149–150.
- Instituto de Meteorología e Hidrología de Panamá. (2024, July 31). Clasificación Climática. IMHPA. <https://www.imhpa.gob.pa/es/clasificacion-climatica>
- Instituto Geográfico Nacional Tommy Guardia. (1988). Atlas nacional de la Republica de Panamá (Instituto Geográfico Nacional Tommy Guardia, Ed.; 3rd ed.). Universidad de Panamá.
- Kim, T. W., & Christy, J. H. (2015). A mechanism for visual orientation may facilitate courtship in a fiddler crab. *Animal Behaviour*, 101, 61–66. <https://doi.org/10.1016/J.ANBEHAV.2014.12.007>
- Kristensen, E. (2008). Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *Journal of Sea Research*, 59(1–2), 30–43. <https://doi.org/10.1016/j.seares.2007.05.004>
- Kwiecinski, B., & D’Croz, L. (2008). El cambio climático y su proyección sobre el nivel del mar en la costa del Pacífico de Panamá. *Tecnociencia*, 10(2), 95–101. <https://doi.org/10.48204/NH>
- Landstorfer, R. B., & Schubart, C. D. (2010). A phylogeny of Pacific fiddler crabs of the subgenus *Minuca* (Crustacea, Brachyura, Ocypodidae: *Uca*) with the description of a new species from a tropical gulf in Pacific Costa Rica. *Journal of Zoological Systematics and Evolutionary Research*, 48(3), 213–218. <https://doi.org/10.1111/j.1439-0469.2009.00554.x>
- Lavezzo, B., Kinoshita, A., Figueiredo, A. M. G., Pinheiro, M. M. F., & Santana, W. (2020). Detection of rare-earth elements using fiddler crabs *Leptuca leptodactyla* (Crustacea: Ocypodidae) as bioindicators in mangroves on the coast of São Paulo, Brazil. *Science of The Total Environment*, 738, 139787. <https://doi.org/10.1016/J.SCITOTENV.2020.139787>
- Lazarus, J. F., & Cantera, J. R. (2007). Crustáceos (Crustacea: Sessilia, Stomatopoda, Isopoda, Amphipoda, Decapoda) de Bahía Málaga, Valle del

- Cauca (Pacífico colombiano). *Biota Colombiana*, 8(2), 221–239.
- Lindquist, E. S., Krauss, K. W., Green, P. T., O'Dowd, D. J., Sherman, P. M., & Smith, T. J. (2009). Land crabs as key drivers in tropical coastal forest recruitment. *Biological Reviews*, 84(2), 203–223.
- Lombardo González, R. C. (2023). Predation of the fiddler crab, *Minuca osa* (Brachyura: Ocypodidae), by *Eudocimus albus* (Pelecaniformes: Threskiornithidae) from Ponuga, Veraguas, Panama. *Journal of Marine and Coastal Sciences*, 15(2), 2–17. <https://doi.org/10.15359/REVMAR.15-2.1>
- Lombardo, R. C. (2022). First record of the Fiddler Crab, *Minuca osa* from the Eastern Montijo Gulf, Panama. *Revista Ciencias Marinas y Costeras*, 14(2), 27–35. <https://doi.org/10.15359/revmar.14-2.2>
- Lombardo, R. C. (2023). Behavior and activity pattern of *Minuca osa* (Brachyura Ocypodidae) from Ponuga, Veraguas, Panama. *Biología, Ciencia y Tecnología*, 16, 1194–1210. <https://doi.org/10.22201/fesi.20072082e.2023.16.85678>
- Lombardo, R. C. (2024). New records of *Minuca zaca* (Brachyura: Ocypodidae) in the Gulfs of Montijo and Parita, Panama. *Revista Ciencias Marinas y Costeras*, 16(1), 33–42. <https://doi.org/10.15359/revmar.16-1.2>
- Lourie, S. A., & Vincent, A. C. J. (2004). Using biogeography to help set priorities in marine conservation. *Conservation Biology*, 18(4), 1004–1020. <https://doi.org/10.1111/J.1523-1739.2004.00137.X>
- Mi Ambiente. (2024, March 15). Las playas El Agallito y El Retén, designadas como un sitio de importancia internacional para la conservación de las aves playeras. <https://www.miambiente.gob.pa/las-playas-el-agallito-y-el-reten-designadas-como-un-sitio-de-importancia-internacional-para-la-conservacion-de-las-aves-playeras/>
- Mokhtari, M., Ghaffar, M. A., Usup, G., & Cob, Z. C. (2015). Determination of key environmental factors responsible for distribution patterns of Fiddler Crabs in a tropical mangrove ecosystem. *PLoS ONE*, 10(1), 17. <https://doi.org/10.1371/journal.pone.0117467>
- Peer, N., Rishworth, G. M., Miranda, N. A. F., & Perissinotto, R. (2018). Biophysical drivers of fiddler crab species distribution at a latitudinal limit. *Estuarine, Coastal and Shelf Science*, 208, 131–139. <https://doi.org/10.1016/j.ecss.2018.05.001>
- Peters, H. M. (1955). Die winkgebärde von *Uca* und *Minuca* (Brachyura) in

- vergleichend-ethologischer, -ökologischer und -morphologisch-anatomischer betrachtung. *Zeitschrift Für Morphologie Und Ökologie Der Tiere*, 43(5), 425–500. <http://www.jstor.org/stable/43261927>
- Rathbun, M. J. (1902). Papers from the Hopkins Stanford Galapagos expedition, 1898–1899. VIII. Brachyura and Macrura. *Proceedings of the Washington Academy of Sciences*, 4, 275–292. <http://www.jstor.org/stable/24526068>
- Rathbun, M. J. (1904). Descriptions of three new species of american crabs. *Proceedings of the Biological Society of Washington*, 17, 161–162.
- Rathbun, M. J. (1935). Preliminary descriptions of six new species of crabs from the Pacific Coast of America. *Proceedings of The Biological Society of Washington*, 48, 49–51.
- Rosenberg. (2023, August 28). Fiddler Crab Guide: Pacific Coast of the Americas. INaturalist. <https://www.inaturalist.org/journal/msr/82286-fiddler-crab-guide-pacific-coast-of-the-americas>
- Rosenberg, M. S. (2001). The Systematics and Taxonomy of Fiddler Crabs: A Phylogeny of the Genus *Uca*. *Journal of Crustacean Biology*, 21(3), 839–869. <https://doi.org/10.1163/20021975-99990176>
- Rosenberg, M. S. (2014). Contextual cross-referencing of species names for fiddler crabs (Genus *Uca*): an experiment in cyber-taxonomy. *PLoS ONE*, 9(7), e101704. <https://doi.org/https://doi.org/10.1371/journal.pone.0101704>
- Rosenberg, M. S. (2019). A fresh look at the biodiversity lexicon for fiddler crabs (Decapoda: Brachyura: Ocypodidae). Part 1: Taxonomy. *Journal of Crustacean Biology*, 39(6), 729–738. <https://doi.org/10.1093/JCBIOL/RUZ057>
- Rosenberg, M. S. (2020). A fresh look at the biodiversity lexicon for fiddler crabs (Decapoda: Brachyura: Ocypodidae). Part 2: Biogeography. *Journal of Crustacean Biology*, 40(4), 365–383. <https://doi.org/10.1093/jcbiol/ruaa029>
- Shih, H.-T., Ng, P. K. L., Davie, P. J. F., Schubart, C. D., Türkay, M., Naderloo, R., Jones, D., & Liu, M.-Y. (2016). Systematics of the family Ocypodidae Rafinesque, 1815 (Crustacea: Brachyura), based on phylogenetic 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.
- Shih, H. Te, Ng, P. K. L., & Christy, J. H. (2015). *Uca* (Petruca), a new subgenus for

- the rock fiddler crab *Uca panamensis* (Stimpson, 1859) from Central America, with comments on some species of the American broad-fronted subgenera. *Zootaxa*, 4034(3), 471–494. <https://doi.org/10.11646/zootaxa.4034.3.3>
- Shih, H. Te, Ng, P. K. L., Davie, P. J. F., Schubart, C. D., Türkay, M., Naderloo, R., & Jones, D. (2016). Systematics of the family Ocypodidae Rafinesque, 1815 (Crustacea: Brachyura), Based on phylogenetic 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(July), 139–175.
- Silveira, L. F., Beisiegel, B. de M., Curcio, F. F., Valdujo, P. H., Dixo, M., Verdade, V. K., Mattox, G. M. T., & Cunningham, P. T. M. (2010). Para que servem os inventários de fauna? *Estudos Avançados*, 24(68), 173–207. <https://doi.org/10.1590/S0103-40142010000100015>
- Smith, T. J., Boto, K. G., Frusher, S. D., & Giddins, R. L. (1991). Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuarine, Coastal and Shelf Science*, 33(5), 419–432. [https://doi.org/10.1016/0272-7714\(91\)90081-L](https://doi.org/10.1016/0272-7714(91)90081-L)
- Thurman, C. L., Faria, S. C., & McNamara, J. C. (2013). The distribution of fiddler crabs (*Uca*) along the coast of Brazil: implications for biogeography of the western Atlantic Ocean. *Marine Biodiversity Records*, 6, e1. <https://doi.org/10.1017/S1755267212000942>
- von Hagen, H.-O. (1968). Studien an peruanischen Winkerkrabben (*Uca*). *Zoologische Jahrbücher, Abteilung Für Systematik, Ökologie Und Geographie Der Tiere*, 95(2), 395–468.
- von Prahl, H., & Toro, N. (1985). *Uca (Uca) intermedia* (Crustacea: Brachyura: Ocypodidae) A new Fiddler Crab from the Pacific coast of Columbia. *Zoologischer Anzeiger*, 215(5/6), 274–278.

Annex**Figure 2.**

Male specimens of *Leptuca batuenta*. Panel B: males engaged in ritualized combat with crossed chelae, but not pinching the opponent. The duel concludes with one crab overturned on its carapace or retreating to release the chela. **A-D**: El Agallito.

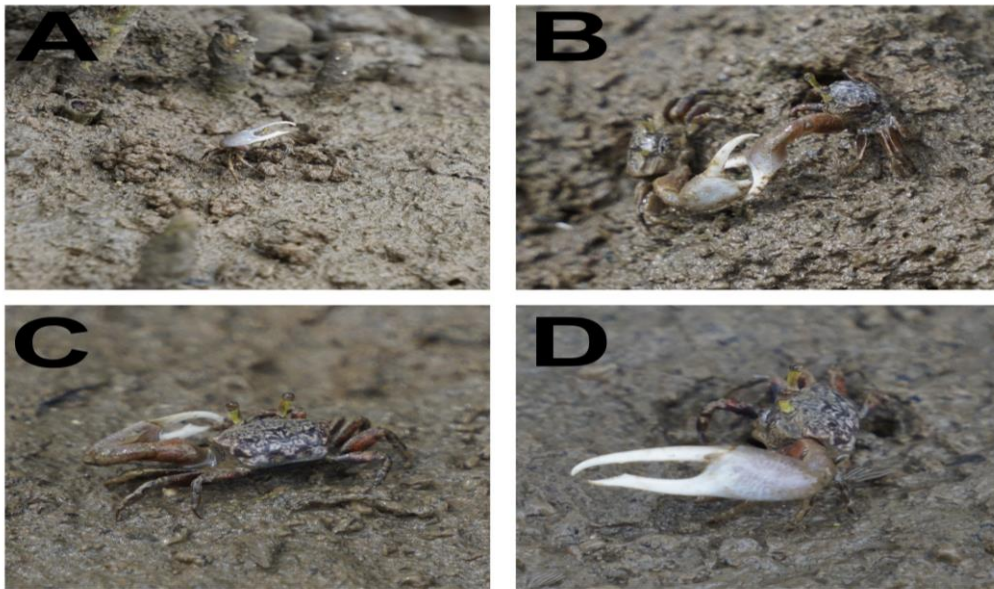


Figure 3.

Images of male specimens of *Leptuca oesterdi*. **A-D**: El Agallito; **E-F**: El Retén

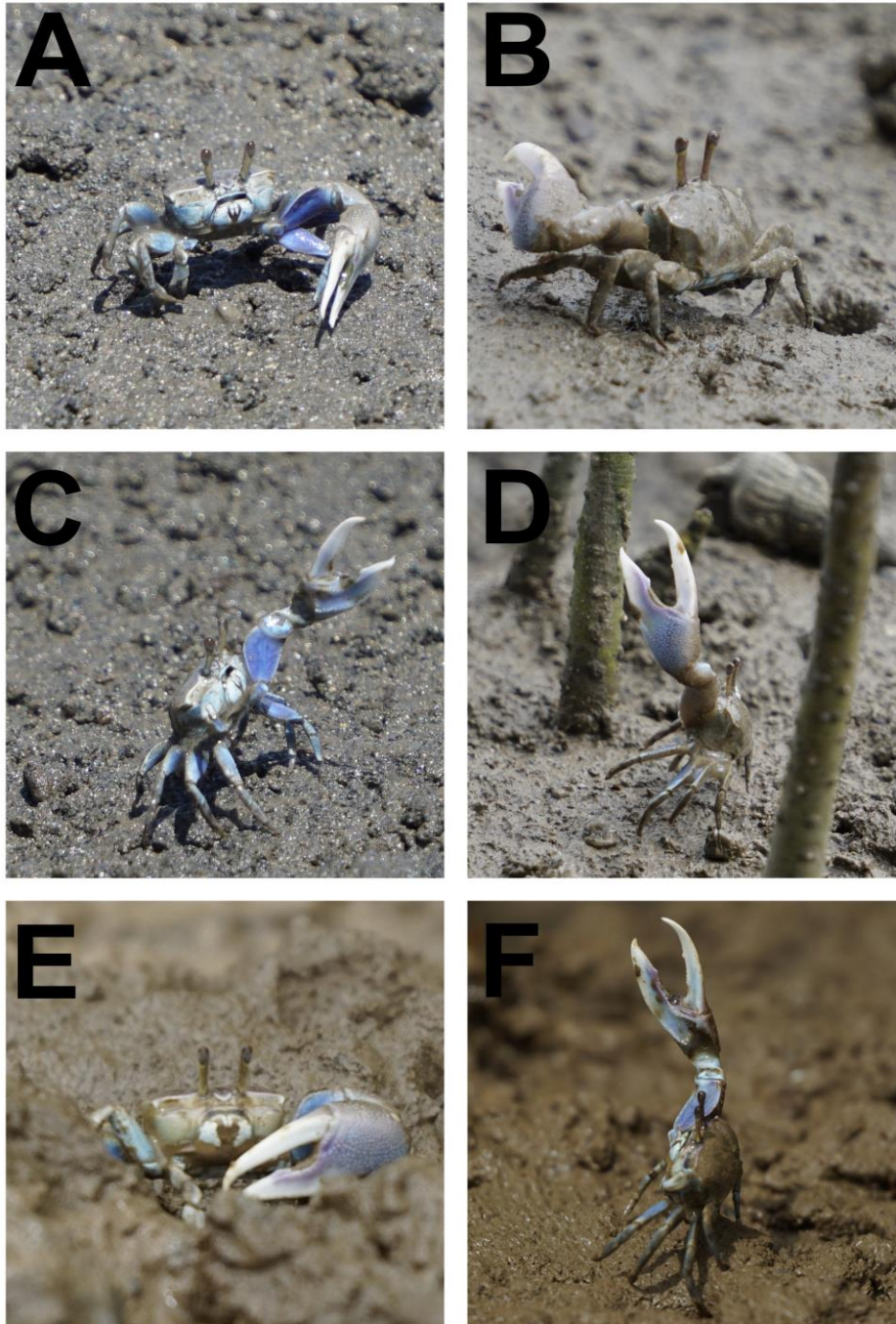


Figure 4.

Images of Leptuca inaequalis specimens. A-C: El Agallito. Panel B includes a female of the species.

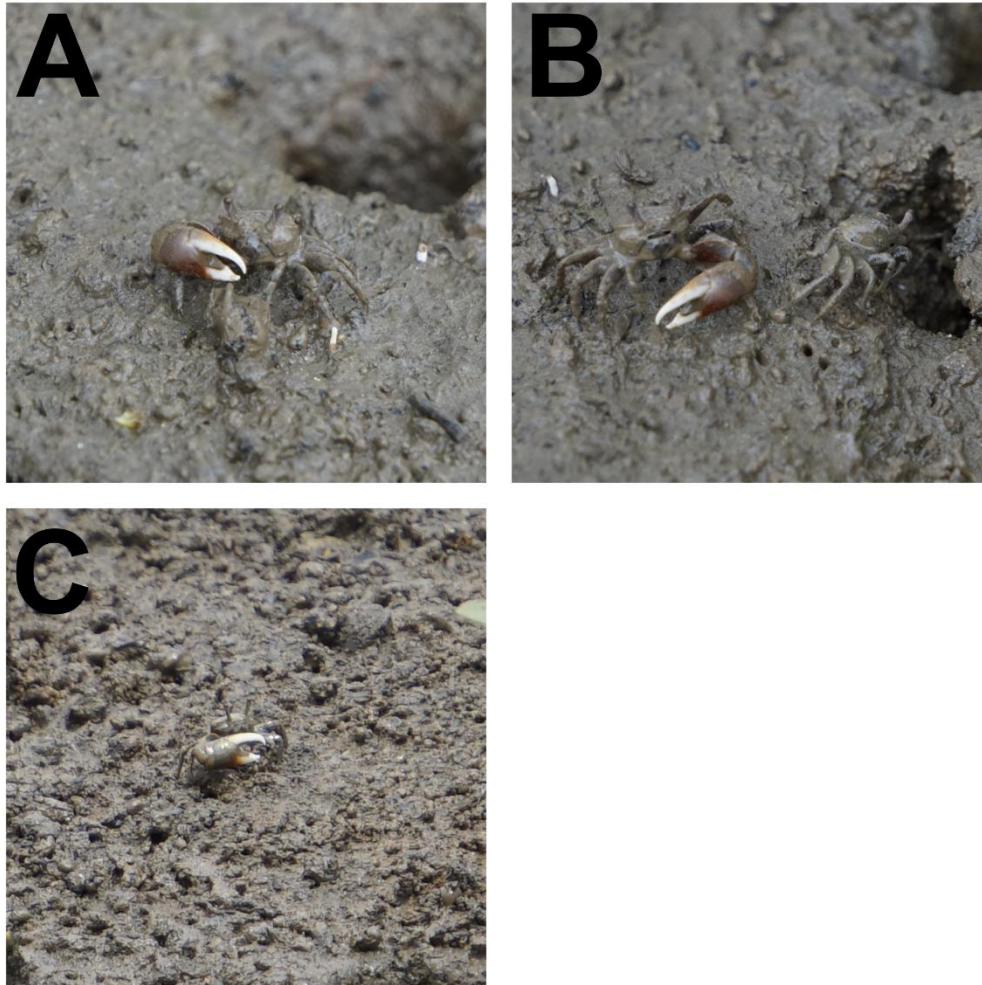


Figure 5.

Images of Leptuca tomentosa specimens. A-C: El Salado; D-F: El Agallito.

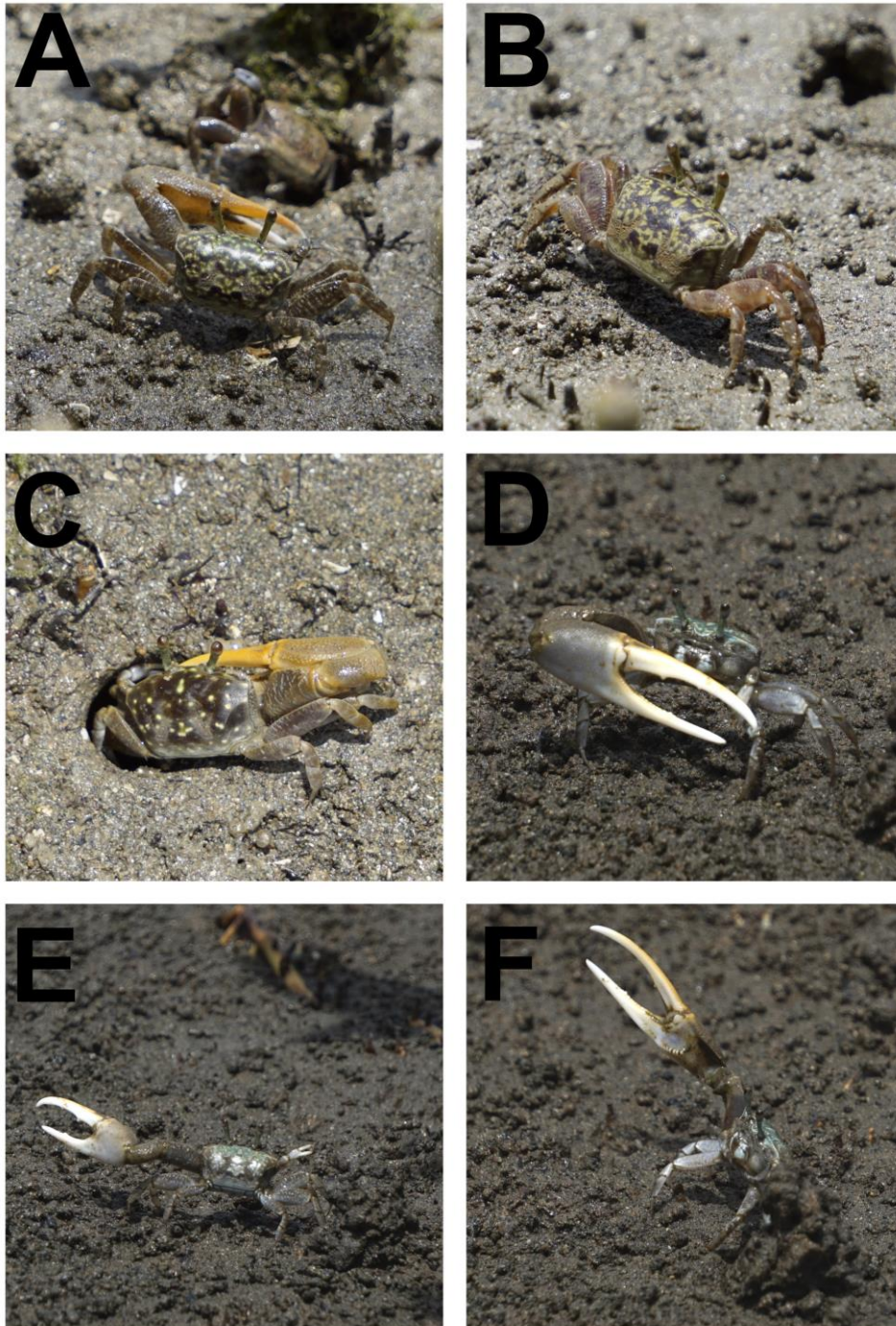


Figure 6.

Images of Leptuca tallanica specimens. A-D: El Salado.

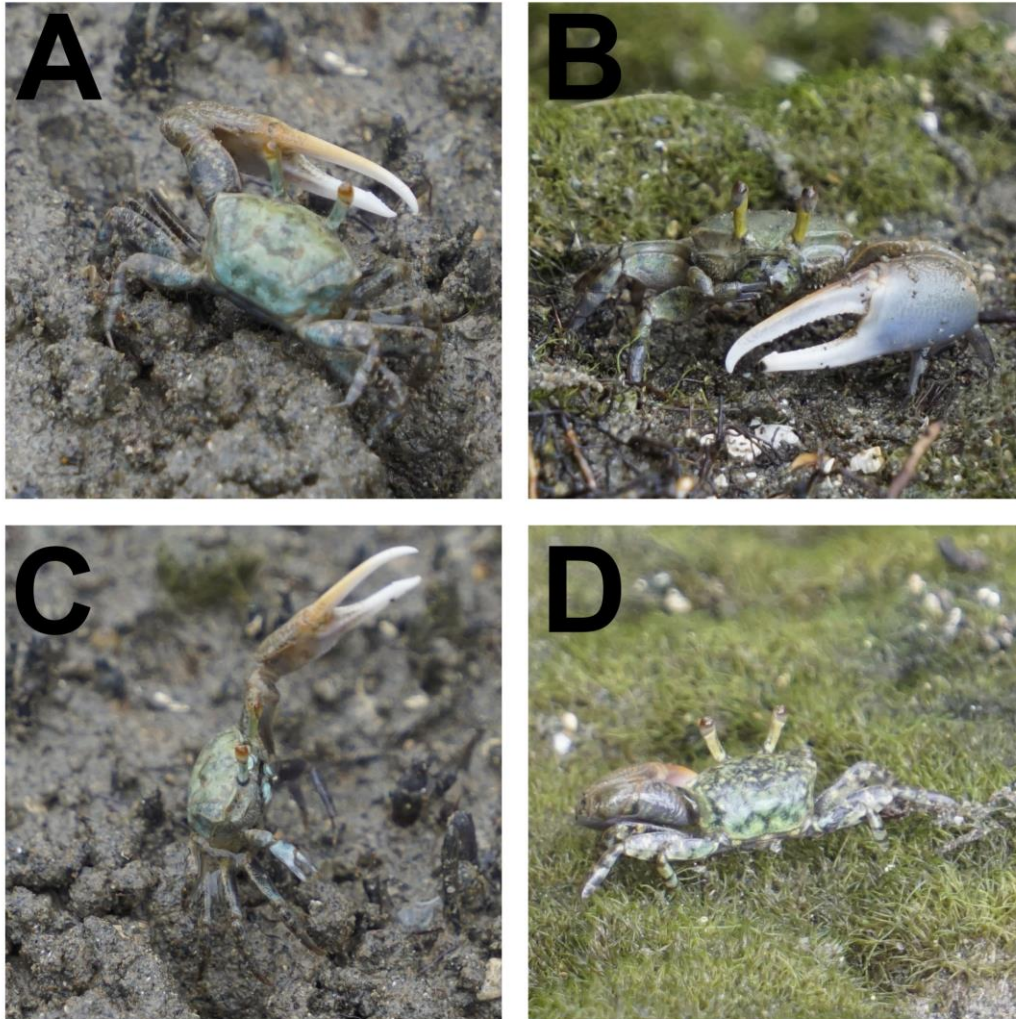


Figure 7.

Images of *Leptuca umbratila* specimens. **A-D:** El Agallito; **B:** El Retén; **C:** Las Comadres. Panel **D** features an image of the female of the species, showcasing its characteristic gray-green coloration and dark olive-green ambulatory appendages.

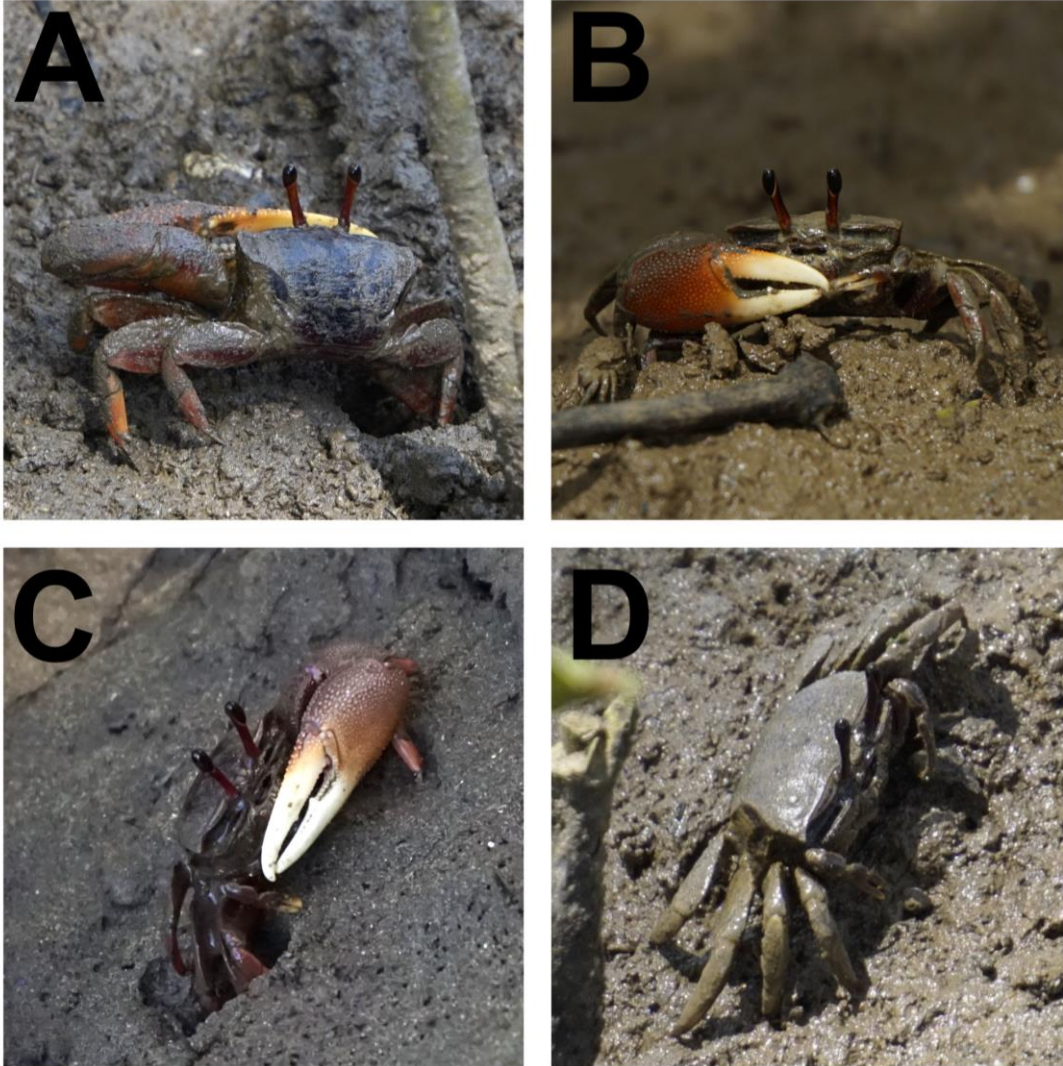


Figure 8.

Images of Leptuca festae specimens. A-C: El Agallito; D-F: El Retén. Panel C includes an image of the female of the species.

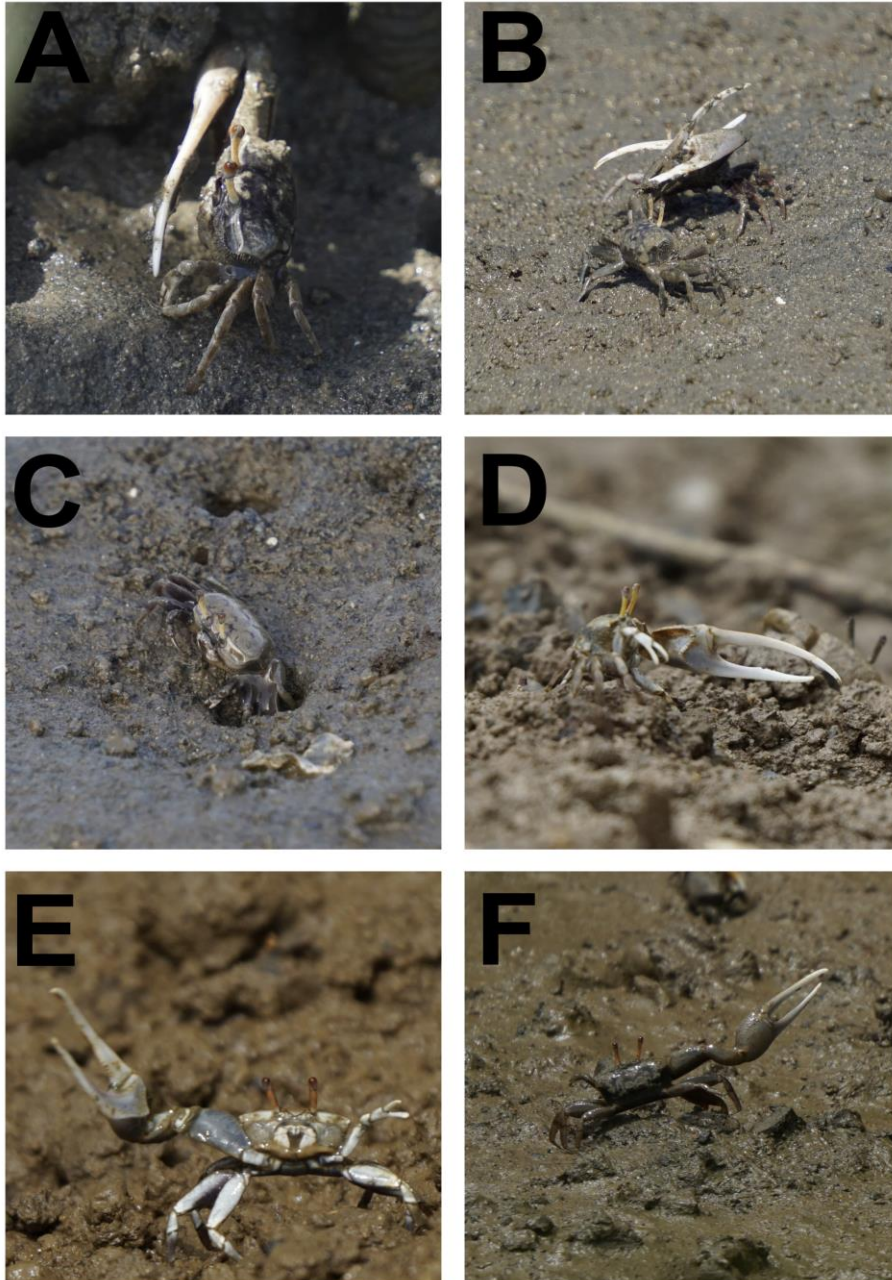


Figure 9.

Images of Leptuca beebei specimens. A, B: El Salado; C-F: El Agallito. Panel C features a male with a pillar next to his burrow courting two females.

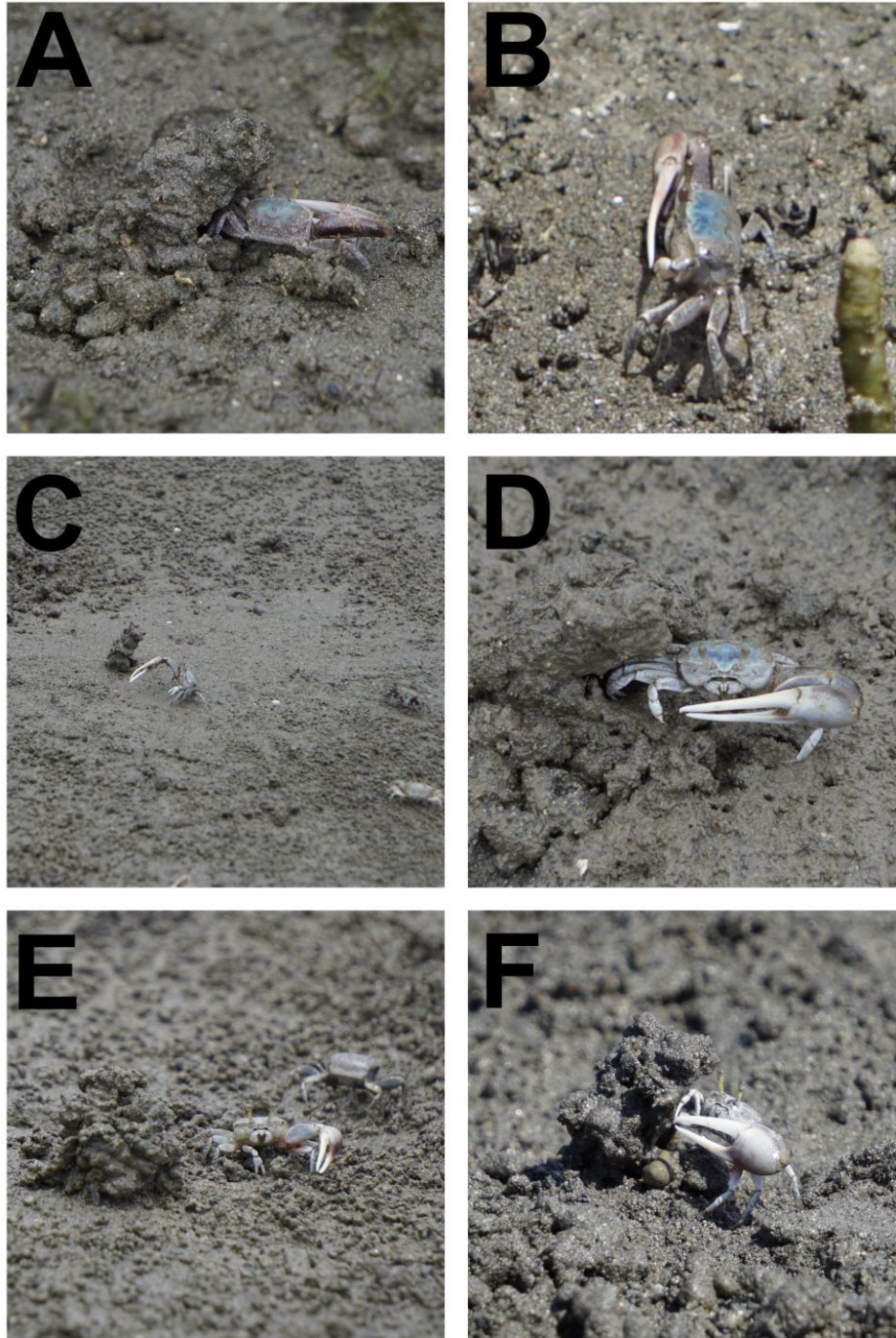


Figure 10.

Images of *Leptuca stenodactylus* specimens. **A:** El Agallito; **B-E:** El Salado; **F:** Las Comadres. Panel **D** features a female of the species.

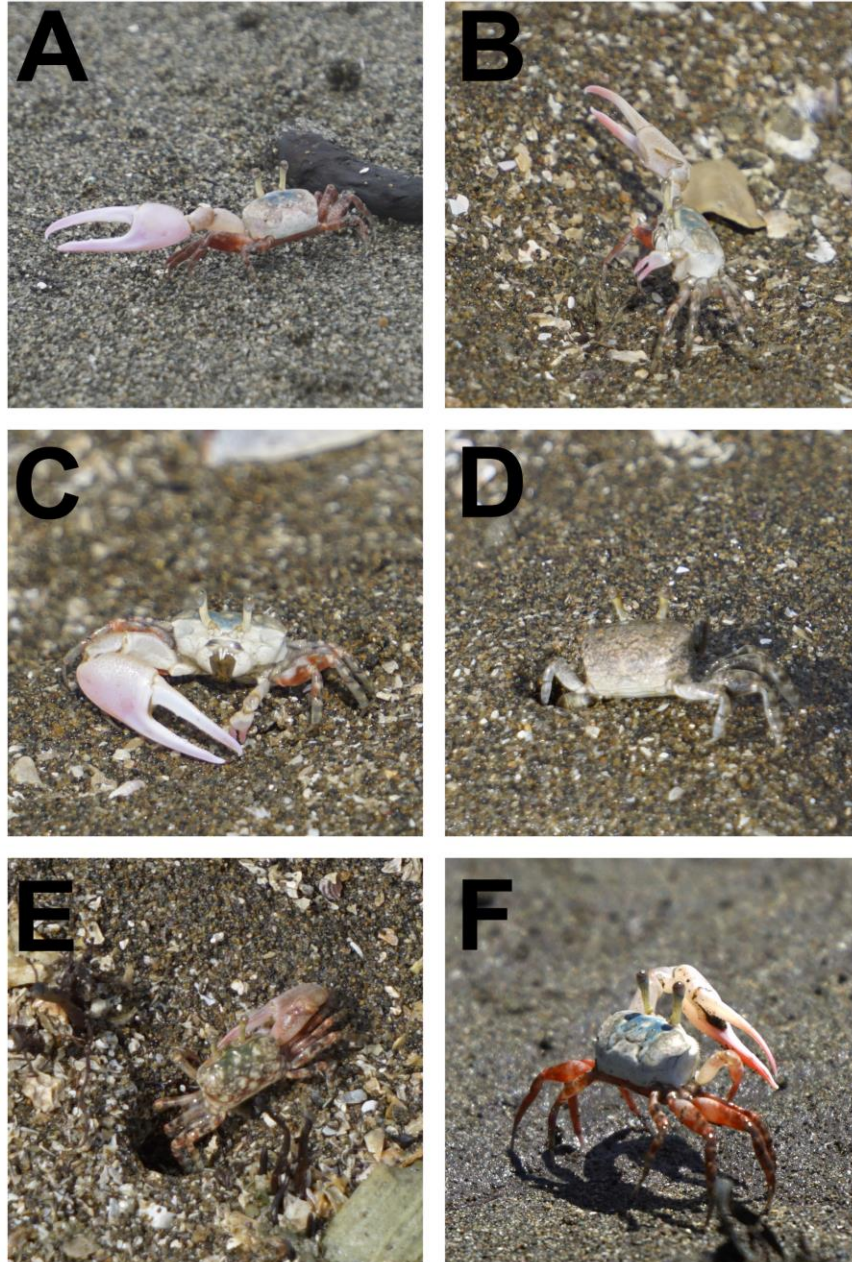


Figure 11.

Images of Leptuca deichmanni specimens. A, C, F: Las Comadres; B: El Uverito; D, E: El Agallito.

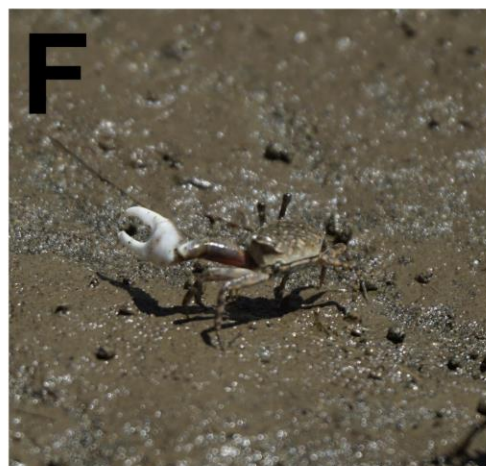
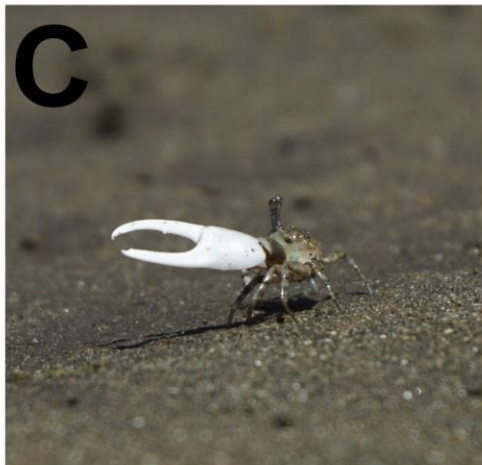


Figure 12.

Images of Leptuca terpsichores specimens. A-D: El Agallito; E: El Retén; F: Las Comadres.

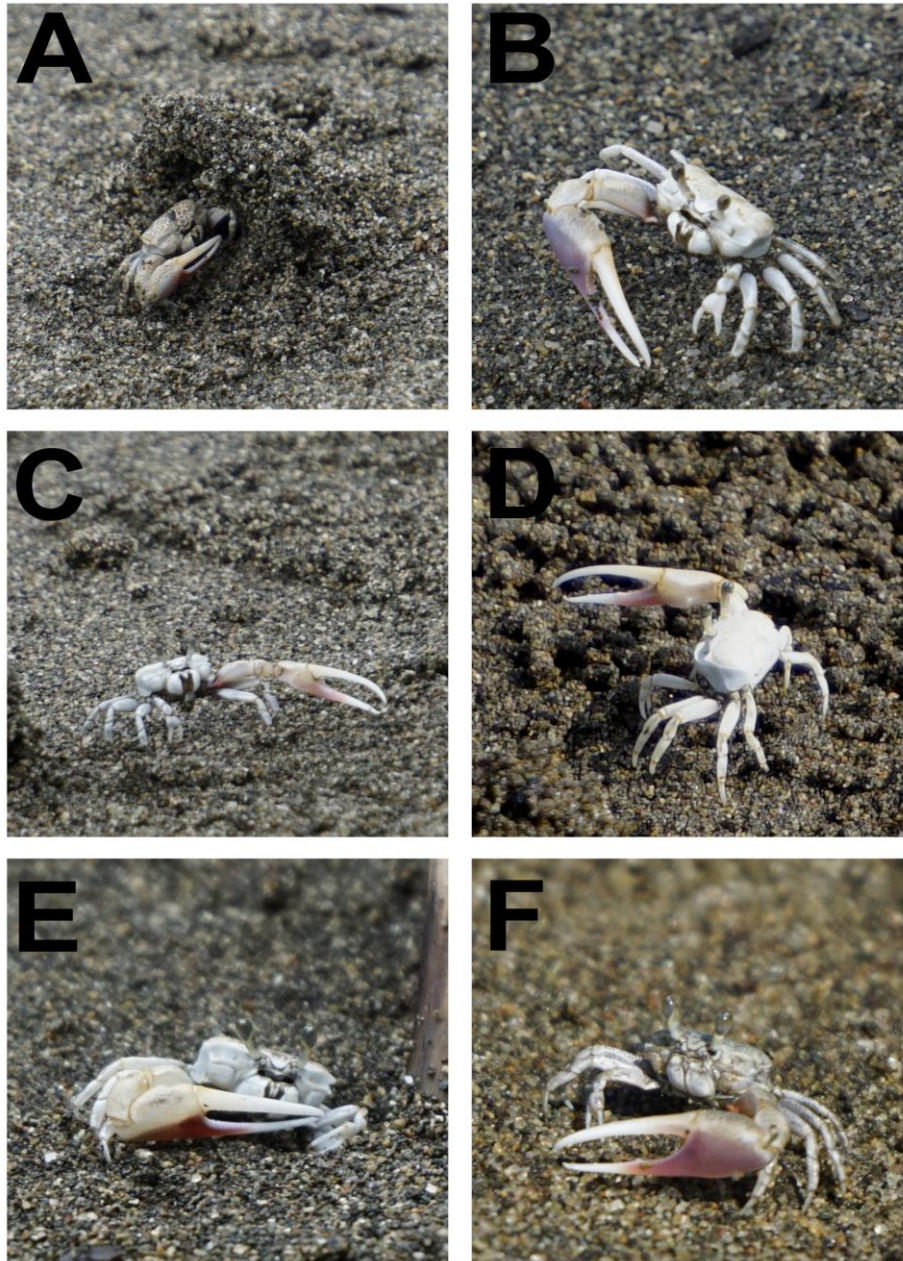


Figure 13.

Images of Leptuca latimanus specimens. A, B: El Salado; C: Los Aromos; D, F: El Retén; E: El Agallito. Panels E and F feature the female of the species.

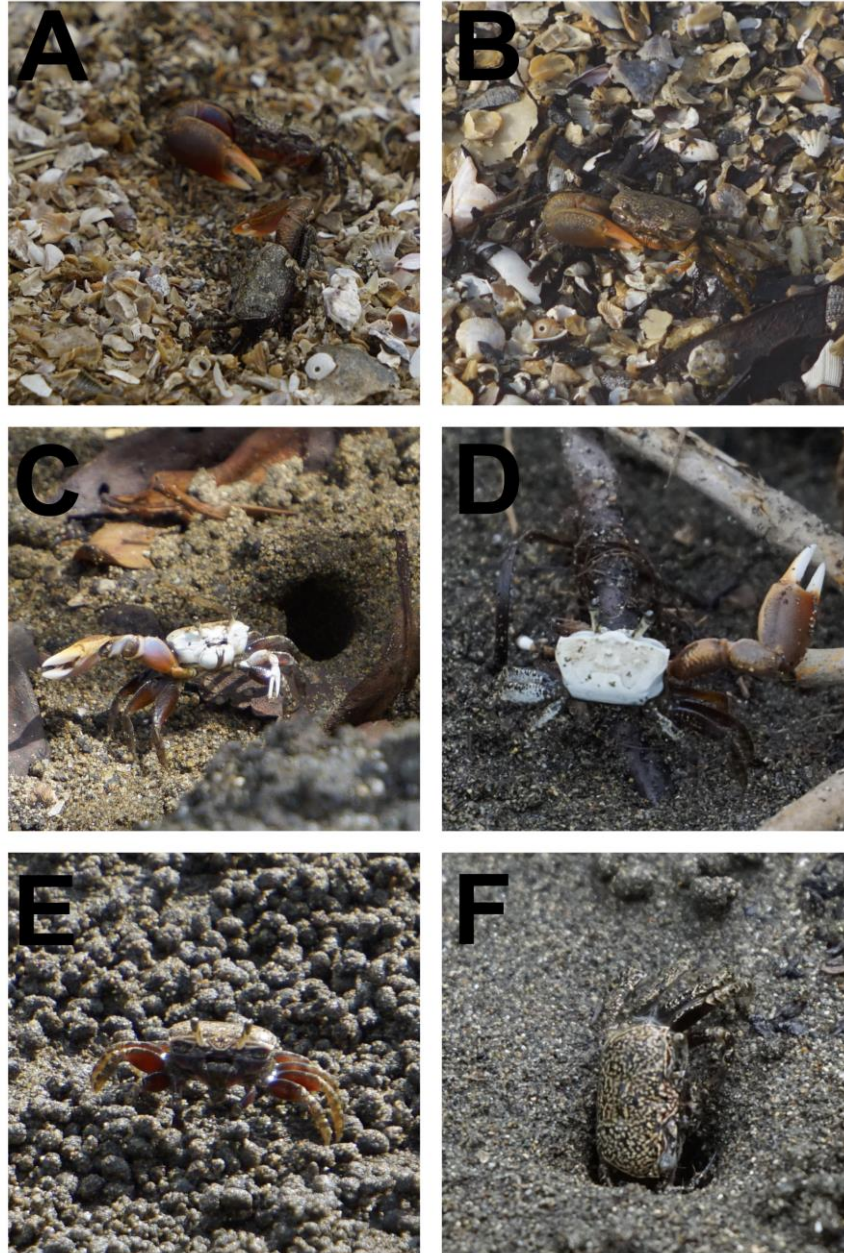


Figure 14.

Images of Uca heteropleura specimens. A-F: El Agallito. Panels E and F include the female of the species.

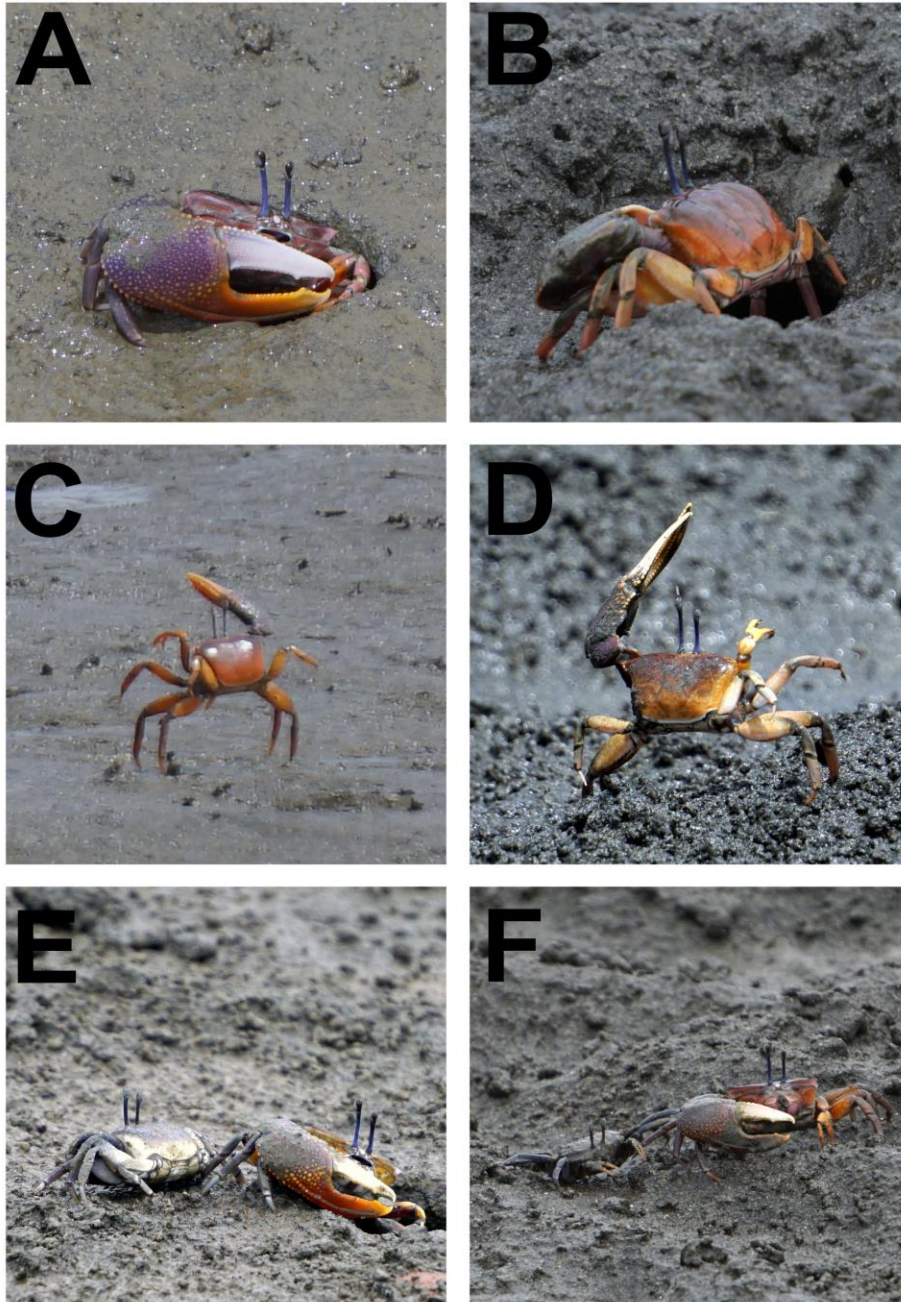


Figure 15.

Images of *Uca intermedia* specimens. **A-F:** El Agallito. Note the short ocular style on the side of the major claw.



Figure 16.

Specimens of Uca ornata. A-F: El Agallito. Panel E shows a young male with residual colors, while panel F displays the female of the species.

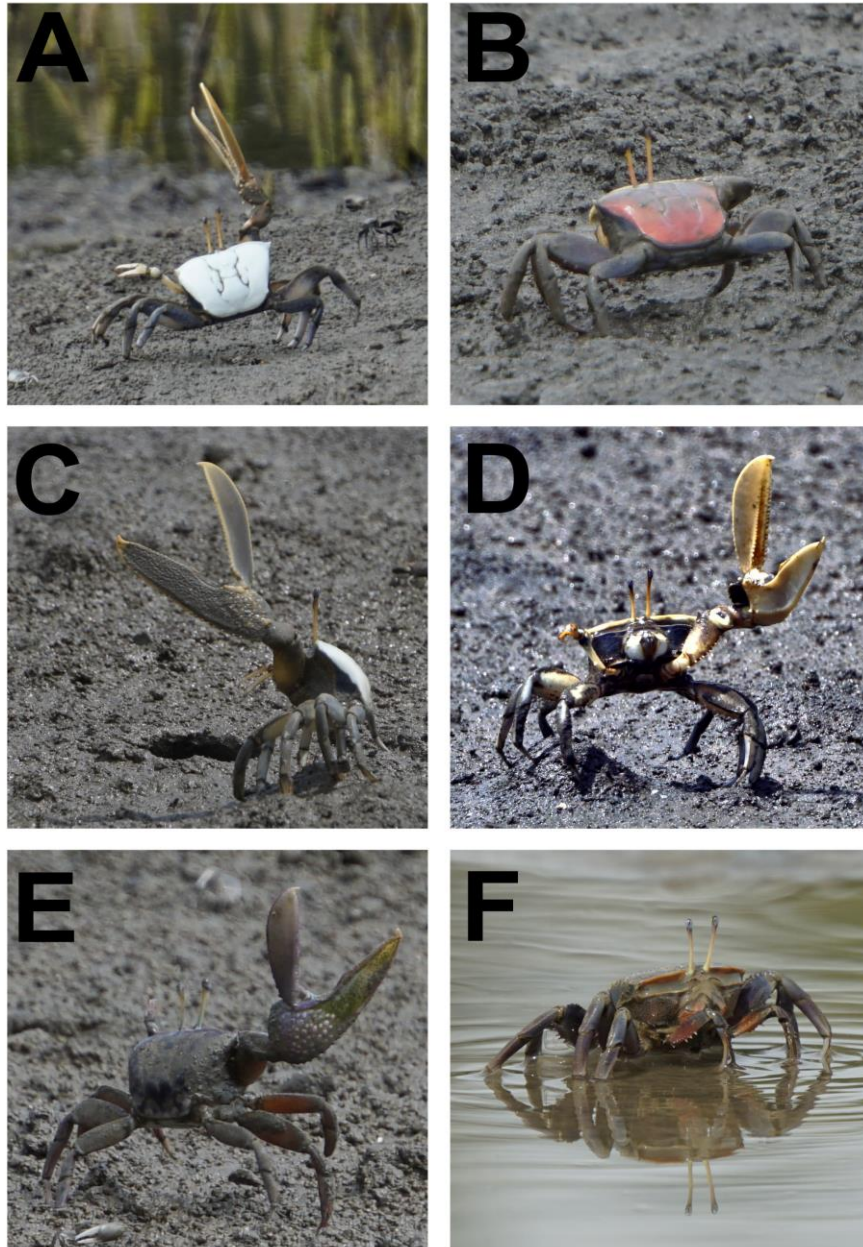


Figure 17.

Images of specimens of *Uca princeps*. **A-C, F:** El Agallito; **D, E:** Los Aromos.

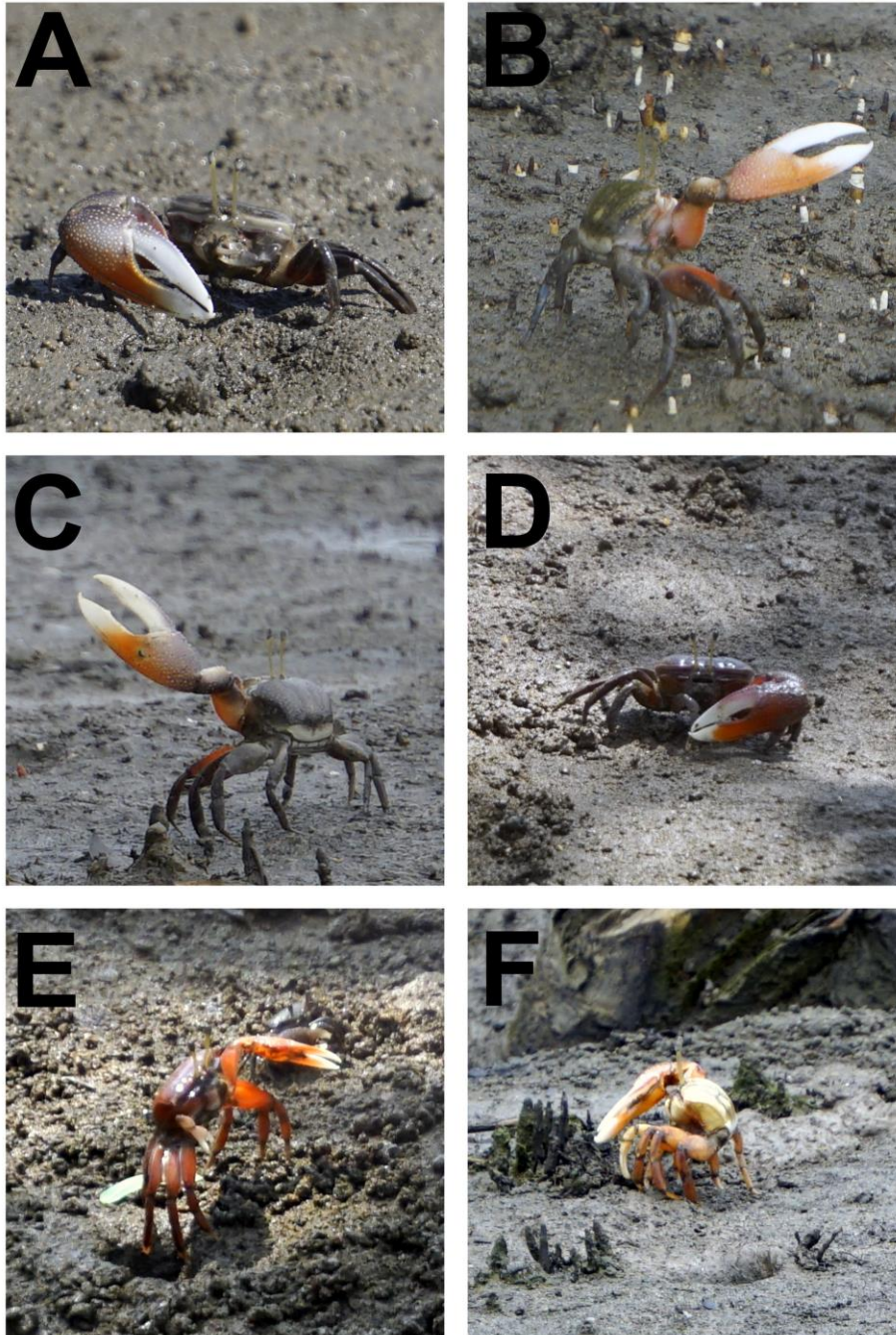


Figure 18.

Images of specimens of Uca stylifera. A, D, E: El Agallito; B, C, F: El Salado. Panel F shows the female of the species.

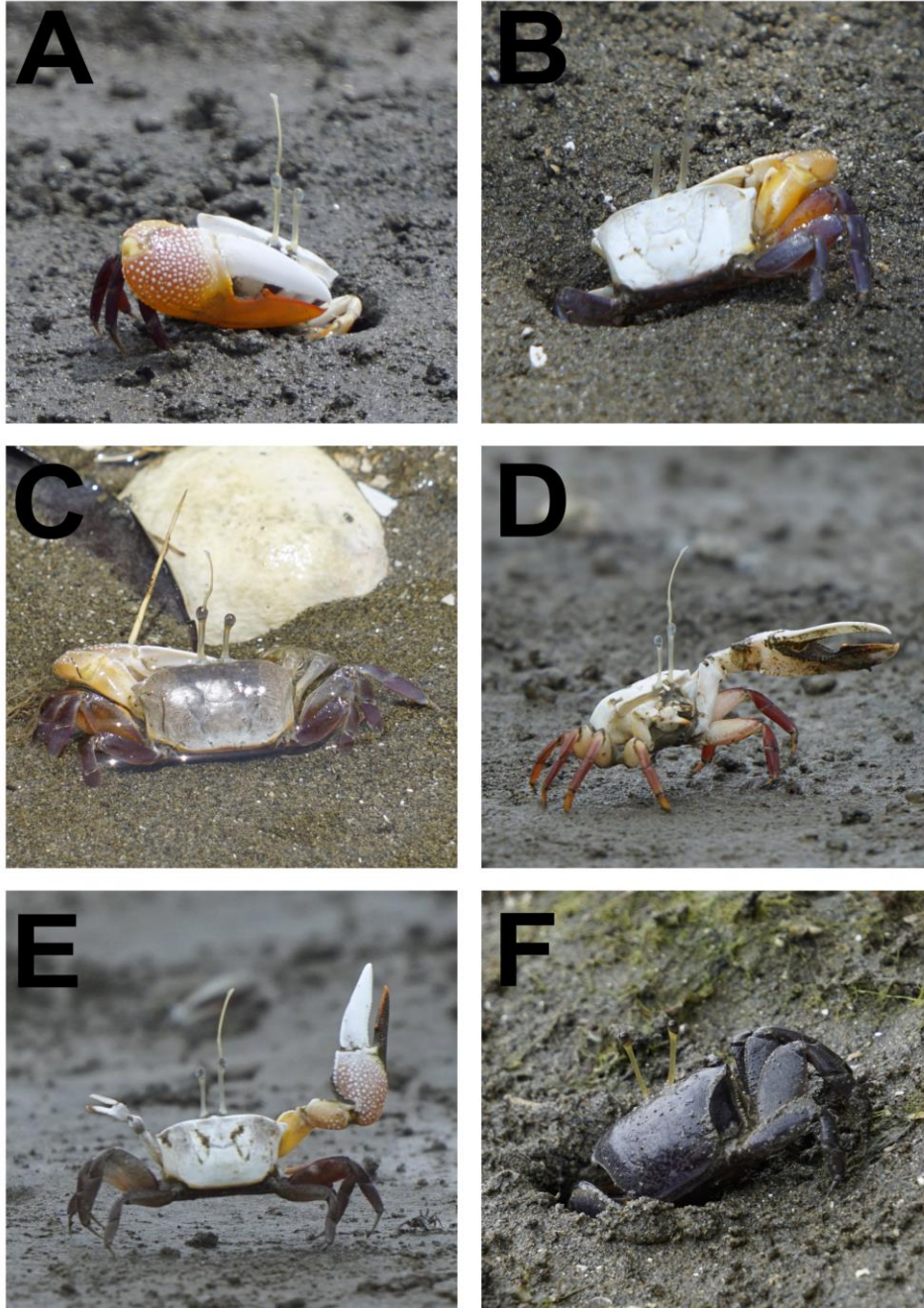


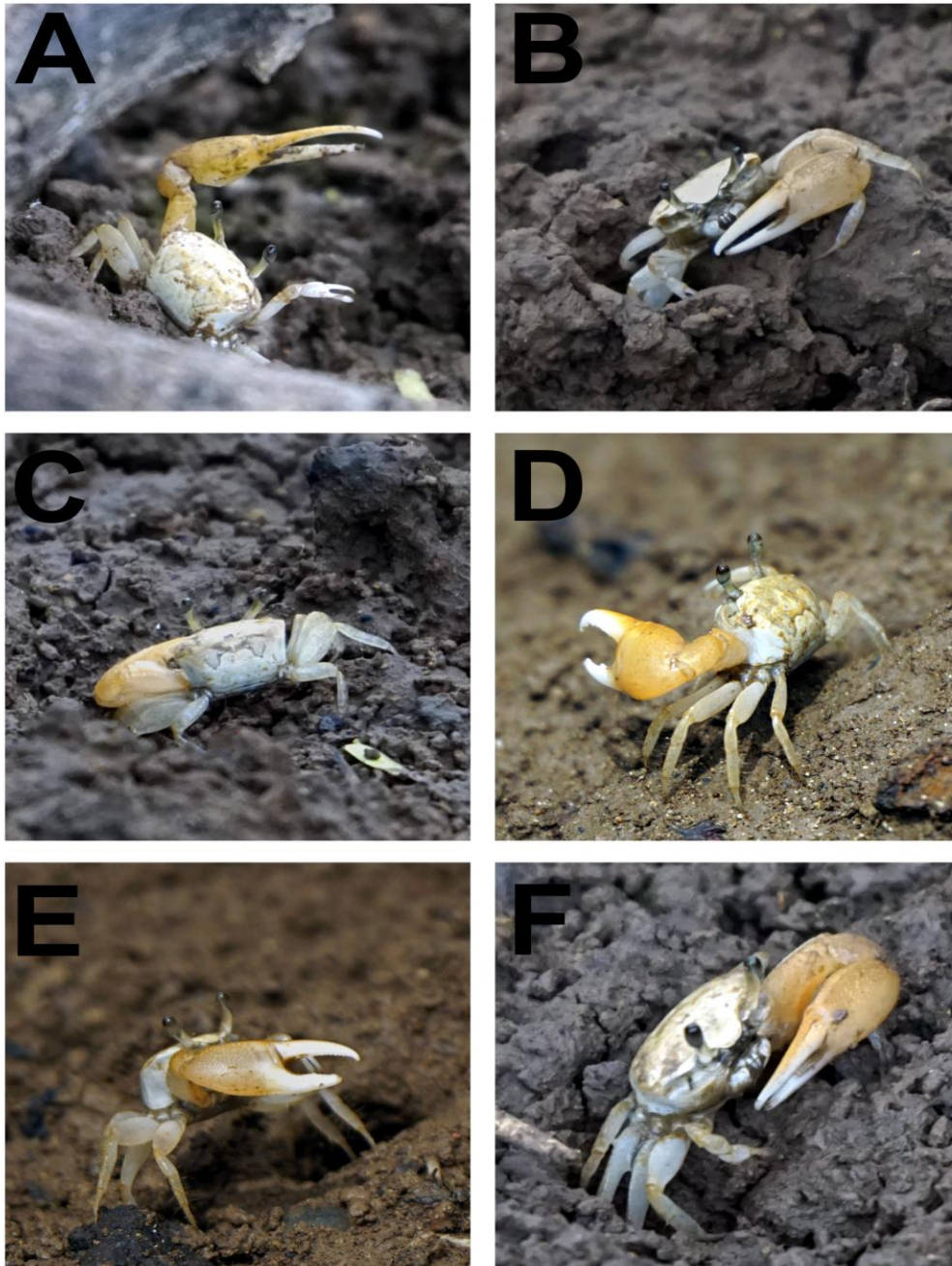
Figure 19

Image of the female of the species Minuca argilicola captured at Playa Las Comadres.



Figure 20

Specimens of *Minuca galapagensis* of the "white" morphotype. **A-F**, El Retén.

**Figure 21**

Images of specimens of *Minuca galapagensis* of the "red" morphotype. **A, C**, El Salado; **B**, El Agallito; **D**, El Retén (female of the species).

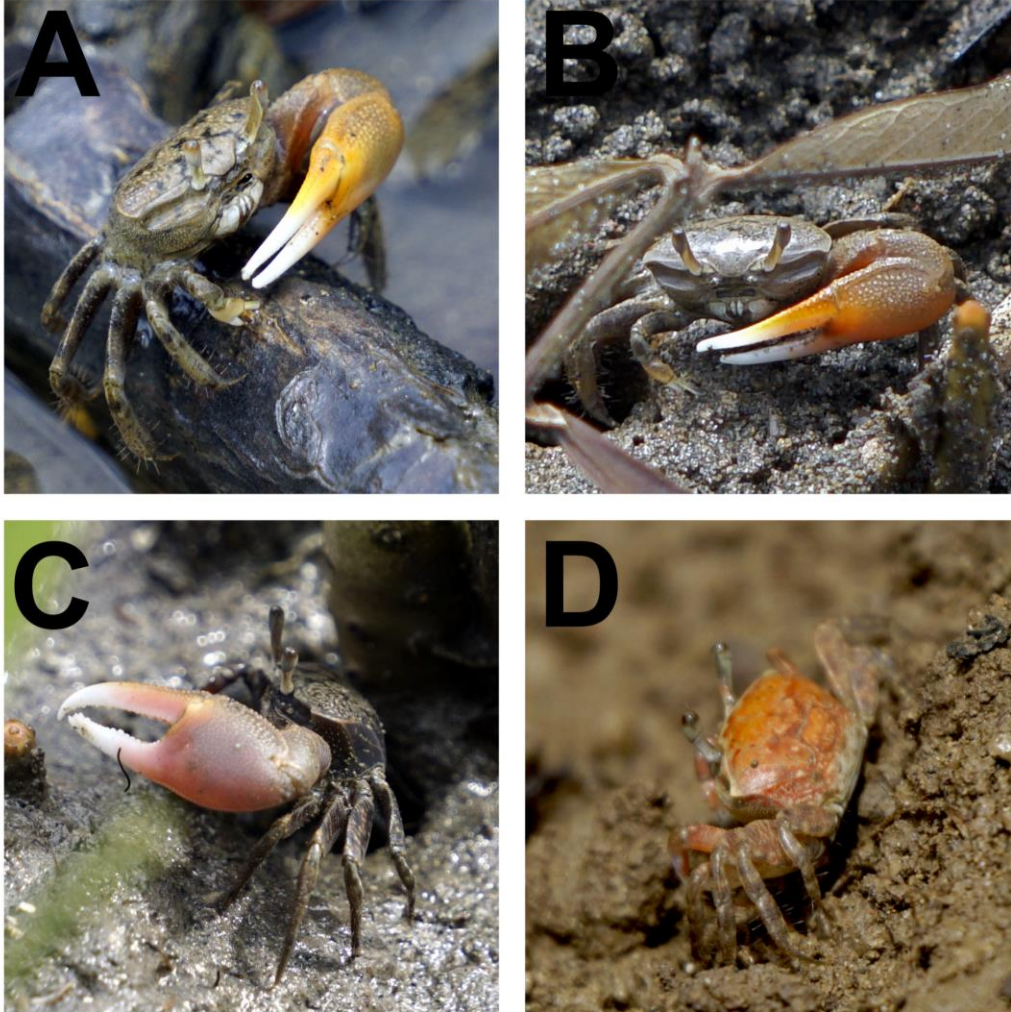


Figure 22

Specimens of *Minuca herradurensis*. **A**, El Salado; **B-C, E-F**, El Retén; **D**, Los Aromos (female of the species).



Figure 23

Image of specimens of *Minuca zaca*. **A**, Los Aromos; **B-D**, El Retén.

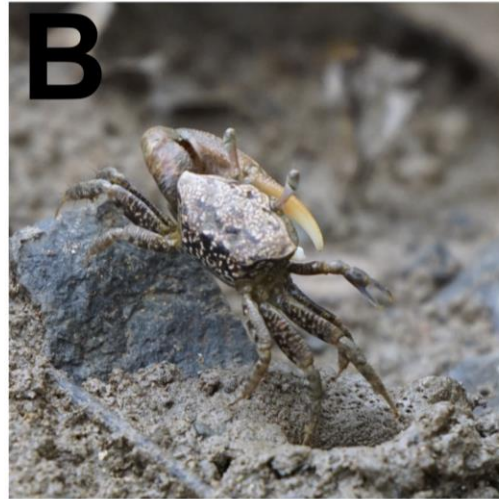


Figure 24

Image of specimens of Petruca panamensis. A-D, El Salado. Panels C and D show females of the species.

